

Chapter 8

RODENTS AND LAGOMORPHS

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INTRODUCTION

Historically, large numbers of wild animals ranged freely over western rangelands of North America; however, the westward expansion of European colonists has gradually brought most of this region under varying degrees of agricultural management. Large scale ranching and irrigated farming displaced buffalo (*Bison bison*) and other wildlife in many areas (Conklin 1928, Fuller and Hafen 1957). This has changed wildlife habitat by producing areas of monocultural crops and emphasizing special range management requirements for livestock. Until the 1840's there was no significant livestock grazing in the West. Today grazing by livestock is a common and economically important practice through much of the western United States, with an estimated 70% of the land in 11 western states subjected to grazing at some time during the year (Mackie 1978). Livestock management practices have been in a rapid state of evolution since the 1800s; from simply placing livestock on a range until the forage was gone, to development of increasingly sophisticated systems of pasture deferment, pasture rotation, and habitat modifications that are designed to stimulate plant productivity, improve efficiency in forage utilization, and avoid overgrazing.

For many years, scientists have been investigating these new interactions among man, wildlife, and rangeland, yet there are relatively few definitive studies of the effects of grazing or of selective grazing systems on rodents and lagomorphs. Although these small mammals are significant wildlife components in all rangeland habitats in North America, research on them has lagged behind more obvious faunal components such as big game and game birds. We know relatively little about the distribution and population abundance of small mammals prior to the onset of grazing or about the effects of grazing on small mammal communities. Small mammals have not generally been of concern to range managers, partially because the empirical data on habitat requirements, species interactions, and life his-

tory patterns needed for their proper rangeland management are often lacking. Yet, basic information about the relationships of small mammal species to their habitats and vegetational physiognomy is critical to making informed decisions about further habitat modifications, wildlife management, and rangeland production. Such information would aid development of effective grazing programs where small mammals are a management concern. This chapter will provide information on the known impacts of grazing to rodents and lagomorphs.

The chapter will also discuss ways in which small mammals influence rangelands. In most natural systems, direct impact on vegetation by small mammal consumption is relatively slight because, despite high reproduction rates, increases in small mammal population densities are not rapid enough to take full advantage of the seasonal increase in food supplies (Hayward and Phillipson 1979). And not all primary production in an ecosystem is suitable for or available to small mammals. Grodzinski (1968) defined available primary production as "that food which is easy to find and is being chosen and eaten." Herbivores in most ecosystems remove a very small amount (< 10%) of plant production (Chew and Chew 1970, French et al. 1976), but the proportion of the net primary production available as food to rodents is greatest in grassland ecosystems (Hayward and Phillipson 1979), where rodents commonly remove 30 to 50% of aboveground net primary production (Lacey and Van Poolen 1981, McNaughton 1985). However, consumption alone is a poor index of impact, as the consequences of consumption may exceed the actual amount eaten (Petrušewicz and Macfadyen 1970). Hayward and Phillipson (1979) estimated that the impact of small mammals in grasslands due to consumption may be only 5% of their actual total impact. The indirect effects of grazing by small mammals may include stimulation of production, alteration of plant species composition, changes in plant stature and reproduction, and influence on

rates of nutrient cycling and decomposition. Which of these alternatives occurs is dependent on the species of small mammal involved and its population density (Batzli 1975). Considerable data are available on a few species of large rodents and lagomorphs in the western United States. Throughout western North America, jackrabbits (*Lepus* spp.), ground squirrels (*Spermophilus* spp.), and burrowing rodents such as pocket gophers (*Thomomys* spp. and *Geomys* spp.) are common rangeland residents. Prairie dogs (*Cynomys* spp.) reach considerable numbers locally. Smaller and less visible rodents such as voles (*Microtus* spp.) are widely distributed on western rangelands, and in the Southwest kangaroo-rat (*Dipodomys* spp.) populations sometimes become large. Less data are available on other smaller species of rodents and lagomorphs.

PRAIRIE DOGS

Prairie dogs are large burrowing rodents classified into the black-tailed and the white-tailed groups. Four species of prairie dogs occur in the United States. Black-tailed prairie dogs (*Cynomys ludovicianus*) have reddish-brown fur and black tips on their tails. The 3 species of white-tailed prairie dogs (i.e., the white-tailed prairie dog [*C. leucurus*], Gunnison's prairie dog [*C. gunnisoni*], and the Utah prairie dog [*C. parvidens*]) have a yellowish coloration to their fur, white tips on their tails, and dark eyebrows. All of the prairie dog species are diurnal, colonial, and social. Female prairie dogs have only 1 estrous cycle/year, in mid-winter. Following about a 30-day gestation period 3-5 young are born in March or April and venture above ground at about 4 or 5 weeks of age. Despite their similarities, the ecology, distribution, and associations with rangeland are quite different for black-tailed and white-tailed prairie dogs. Differences can be attributed to differences in population density and habitat occupied by the two groups. Of the 4 species of prairie dogs, only the black-tailed prairie dog has been studied extensively.

Black-tailed Prairie Dogs

Historical Populations. Black-tailed prairie dogs (Fig. 1) occur throughout the Great Plains from the United States-Canada border to northern Mexico and from the Rocky Mountains east to Nebraska, Kansas, and Oklahoma (Fig. 2). They occur at elevations ranging from 915 to 1,830 m. The black-tailed prairie dog is typically associated with short and midgrass prairie; grasses typically found in the vicinity of prairie dog colonies include western wheatgrass (*Agropyron smithii*), buffalograss (*Buchloe dactyloides*), and blue grama (*Bouteloua gracilis*). Prairie dogs dig extensive burrow systems and create large earth mounds 15-20 cm high around the burrow. Burrows form a highly modified environment where temperatures are fairly stable and relative humidity is much higher than on the surface. Black-tailed prairie dogs are highly social and reside in densely populated colonies (King 1955, Koford 1958, Hoogland 1979), where densities average 15 individuals/ha (range = 5-33/ha). Black-tailed prairie dogs do not hibernate in winter, but may remain underground for long periods of time.

Prairie dogs were widespread on the plains through the 1800s. Seton (1929) estimated that in the late 1800s, prairie dog colonies covered 283 million ha and prairie dogs numbered over 5 billion, often occurring in large colonies covering several km² (Merriam 1902, Hollister 1916, Bell 1921). Merriam (1902) reported 1 prairie dog colony in Texas that covered 64,750 km², and had about 400 million prairie dogs. During this period, prairie dogs probably had a profound effect on rangeland. With settlement of the plains regions, conflicts arose with man as prairie dogs destroyed agricultural crops planted on former rangeland and were thought to be in direct competition with livestock for rangeland forage. Merriam (1902) estimated that the quantity of grass consumed by 32 prairie dogs equaled that required by 1 sheep, and that the amount eaten by 256 prairie dogs was sufficient to support 1 cow. Black-tailed prairie dogs have therefore been considered pests on shortgrass and mixed-grass prairies of central North America since the late 1800s (Merriam 1902).

To control prairie dog numbers, effective rodenticides were developed and in the early 1900s millions of hectares were treated with strychnine and other poisoned grains, significantly reducing prairie dog numbers and eliminating most large colonies (Fig. 3). By 1919, after 20 years of control efforts, the



FIGURE 1. Black-tailed prairie dog (*Cynomys ludovicianus*). Photo by K. Fagerstone.

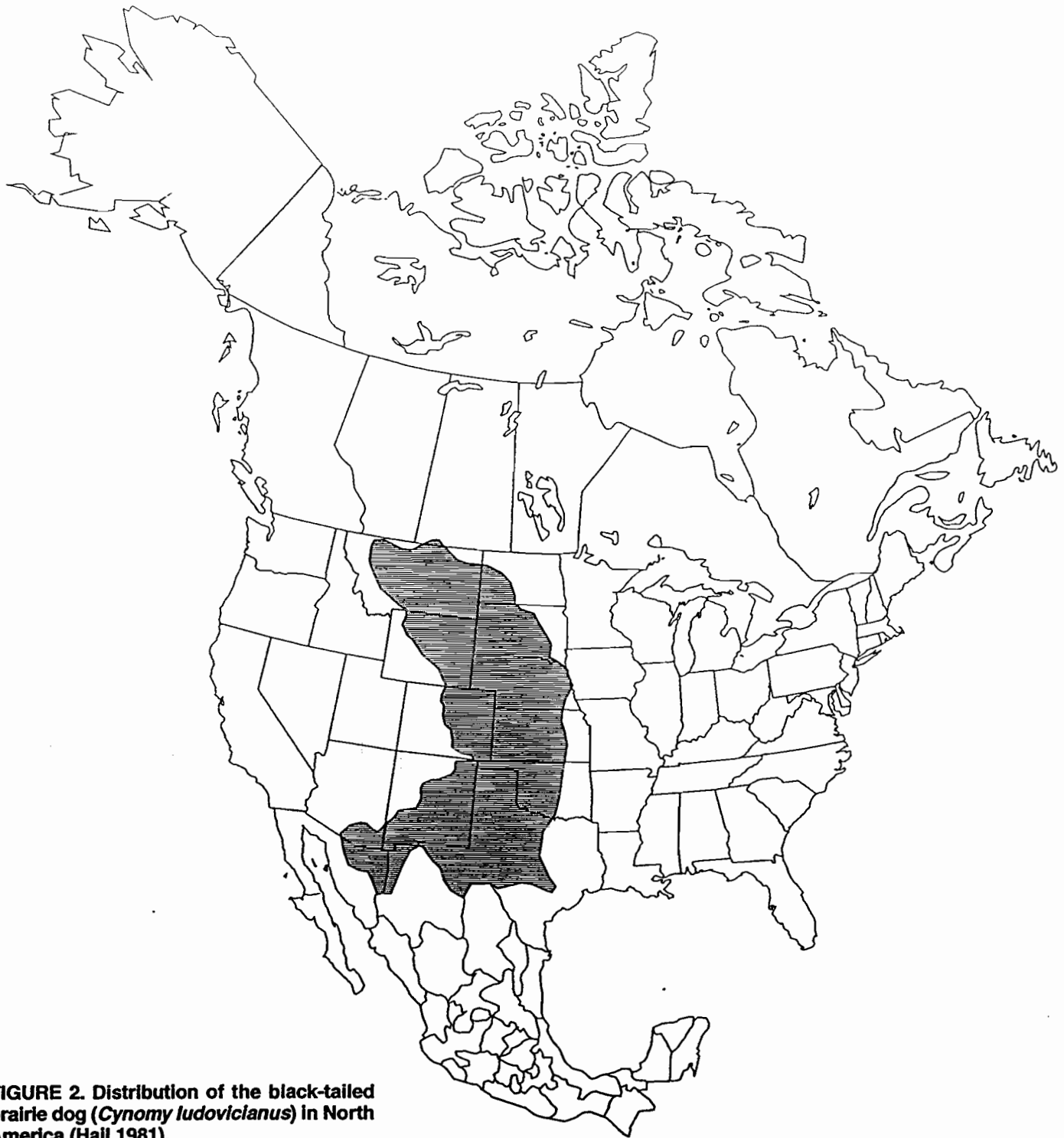


FIGURE 2. Distribution of the black-tailed prairie dog (*Cynomys ludovicianus*) in North America (Hall 1981).

area occupied by prairie dogs was reduced to an estimated 40.5 million ha (Nelson 1919) in the United States and by 1971, they still occupied only 566,000 ha (Cain et al. 1972). The decline was related to federal, state, and local poisoning programs and to changing land use practices that reduced available habitat by converting vast areas of the Great Plains to agriculture and urbanization. Prairie dog populations have increased since 1972, when Presidential Executive Order II 11643 banned the use of secondary poisons on federal lands and thus eliminated most uses of Compound 1080 and strychnine. The largest areas

of land in the United States currently occupied by prairie dogs are federally managed lands.

South Dakota serves as an example of the fluctuations that have occurred in prairie dog populations as a result of the social, economic, political, biological, and climatic changes that have occurred on the Great Plains during the last 100 years (Hanson 1988). In South Dakota the first organized control efforts began in 1914, and in 1919 a rodent control law was passed by the South Dakota Legislature that increased prairie dog control efforts. In 1923, prairie dogs occupied almost 809,000 ha. How-

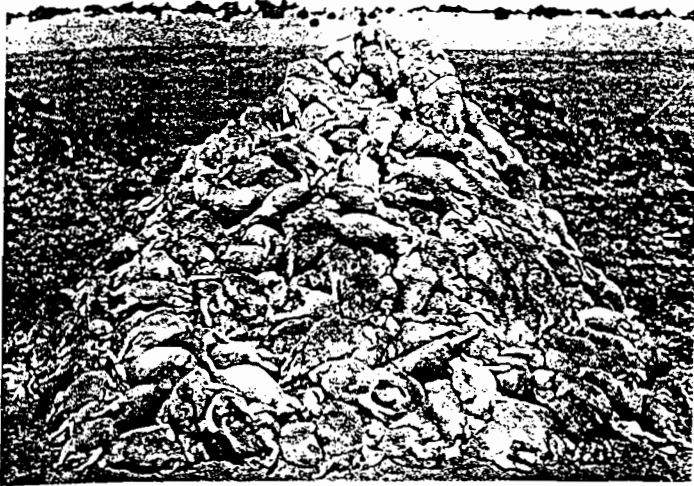


FIGURE 3. Prairie dogs poisoned during the early 1900s, a period when attempts were made to eradicate prairie dogs over most of their range. Photo from Bureau of Biological Survey records.

ever, organized prairie dog control programs continued through the 1920's on private, state, federal, and Indian lands, and by 1930 the prairie dog population had been reduced to widely scattered small towns. In the 1930s, the Dust Bowl forced farmers off agricultural land and depleted existing rangelands, and prairie dog populations increased on these disturbed areas. Utilizing some of the 1930s Federal emergency work programs, control agents pushed prairie dog populations to their lowest recorded level by the 1940s, when only small colonies remained. From 1955 to 1965, prairie dog populations were maintained at about 18,200 ha by use of Compound 1080 baits. The 1972 Executive Order placed most prairie dog control efforts on hold until 1976, when zinc phosphide (that does not have secondary toxicity) was registered for prairie dog control (Tietjen 1976) with the Environmental Protection Agency (EPA). From 1976 to 1979 about 12,000 ha were treated per year (Hanson 1988).

On the Buffalo Grass National Grassland in South Dakota, prairie dog colonies increased about 20%/year after control was discontinued in the early 1970s, from 1,154 ha in 1968 to 14,023 ha in 1978 (K. A. Fagerstone, unpubl. data) (Fig. 4). The increase was so dramatic that a lawsuit was filed in 1980 by the

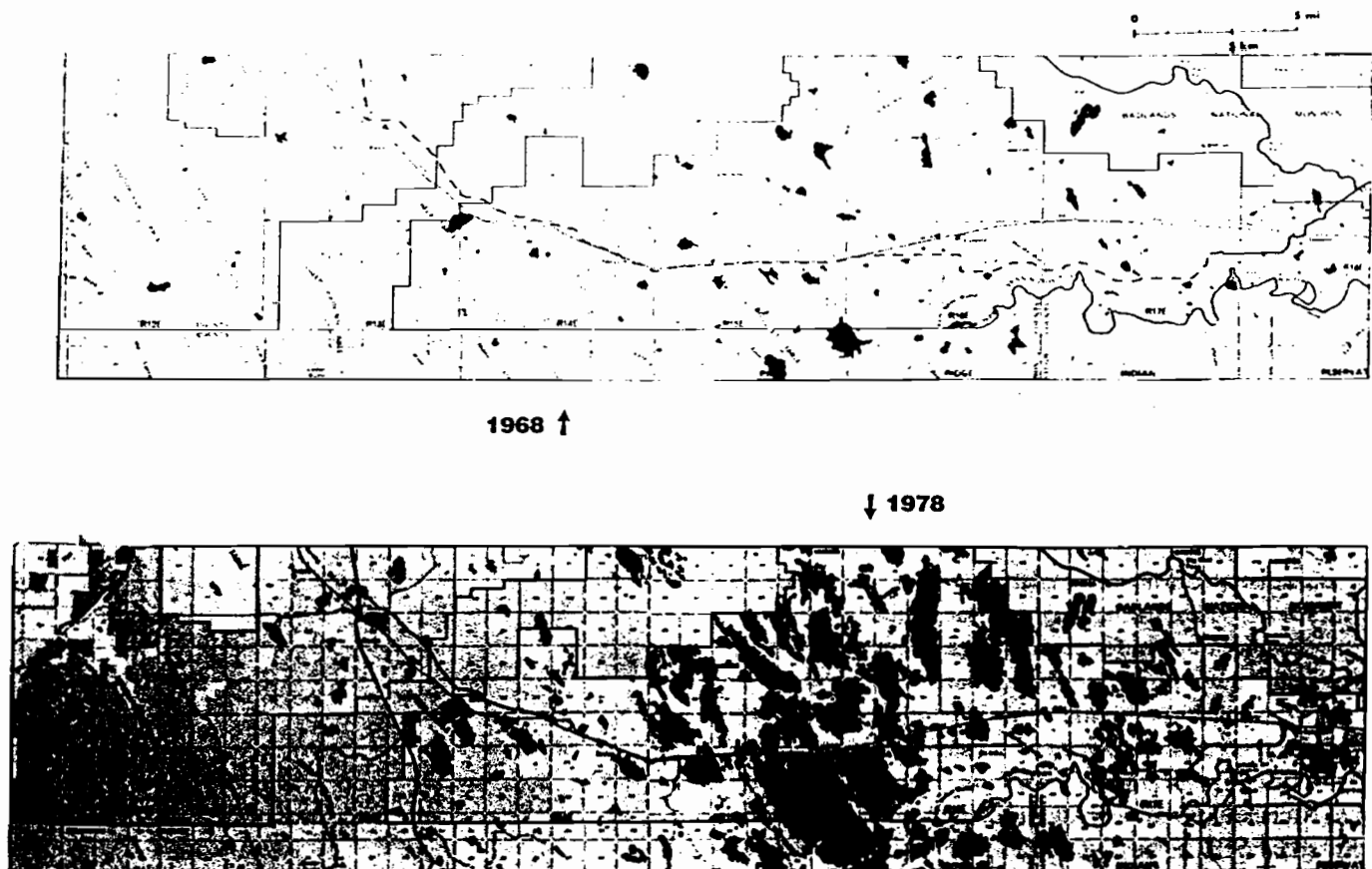


FIGURE 4. Black-tailed prairie dog (*Cynomys ludovicianus*) colony expansion on a 1036 km² area of Buffalo Gap National Grassland, South Dakota, between 1968 and 1978. Colonies are shown in black; each square represents 2.6 km².

American and South Dakota Farm Bureau Federations and others against the United States Forest Service, National Park Service, and Bureau of Indian Affairs contending that these agencies failed to conduct an effective prairie dog control program on lands administered by them and that adjacent private lands were damaged by prairie dogs originating on federal lands. A large-scale control program was conducted as a result of the lawsuit (Schenbeck 1982), and South Dakota passed a weed and pest law in 1984 that allows county boards the authority to declare lands with prairie dogs a public nuisance and to require prairie dog control in response to complaints from neighboring landowners. Prairie dogs now occupy about 324,000 ha in South Dakota. Because the perception is still prevalent with landowners that prairie dogs compete for forage with livestock, massive prairie dog control programs are still common (Schenbeck 1982).

Effects of Range Condition on Prairie Dogs. Many researchers have suggested that prairie dogs colonize sites that have been overgrazed or otherwise disturbed (Koford 1958, Uresk et al. 1982, Coppock et al. 1983a, Uresk and Bjugstad 1983). Black-tailed prairie dogs in particular have been shown to prefer areas with short vegetative cover; low cover apparently allows them to view predators and maintain a complex social system (Slobodchikoff and Coast 1980). Rates of prairie dog colony settlement and expansion have been shown to increase under intense livestock grazing and other human disturbances such as homesteading, fencing, cultivation, and the construction of water impoundments (Osborn and Allan 1949, Uresk et al. 1982, Cincotta 1985, Snell 1985, Cincotta et al. 1987). All of these land management practices reduce height and density of grasses, and provide a desirable environment for prairie dogs to expand and establish new colonies. Prairie dog distribution is correlated to these management practices (Knowles 1982, Cincotta 1985). Uresk et al. (1982) found that prairie dog burrow densities in the Conata Basin of South Dakota increased twice as fast on sites grazed by cattle as on ungrazed sites. Within this area, prairie dog colonies increased at the rate of 20%/year between 1968 to 1978 on the heavily grazed Buffalo Gap National Grassland but only increased 4% on the adjacent ungrazed portions of the Badlands National Monument (K. A. Fagerstone, unpubl. data, Fig. 4).

Effects of Prairie Dogs on Rangeland. Once established, prairie dogs modify the grasslands that they occupy. Because prairie dogs depend on being able to see terrestrial predators from some distance away (Slobodchikoff and Coast 1980), they clip shrubs and other tall vegetation that impede visual detection to a height of only a few centimeters. Vegetation is considerably modified by prairie dog feeding activities and by clipping of unpalatable plants to ground level (King 1955, Koford 1958). In well-established prairie dog colonies (Fig. 5), large areas of bare soil are common (Knowles 1982) and soil temperatures are raised (Archer and Detling 1986). Canopy height in 1 study was decreased by 62% in the first 2 years of colonization (Archer et al. 1987). Prairie dogs are thus able to maintain a low height vegetative community where species composition, biomass, and productivity of vegetation differ from uncolonized areas

(Osborn and Allan 1949, King 1955, Bonham and Lerwick 1976, Dalsted et al. 1981, Coppock et al. 1983b).

Negative effects of prairie dog colonization on grassland productivity include decreased plant biomass, changes in plant composition from grasses to forbs, a shift toward C4 photosynthetic species, and higher silicon concentrations in forage. Prairie dogs generally reduce total plant biomass, particularly of native perennial grasses (Crocker-Bedford 1976, Hansen and Gold 1977, Crocker-Bedford and Spillett 1977, Knowles 1982, Coppock et al. 1983b, Archer et al. 1984, Uresk 1984). They can clip and consume 24 to 90% of the primary production of a site (Osborn and Allan 1949, Hansen and Gold 1977, Crocker-Bedford and Spillett 1977). Koford (1958) found that range condition on prairie dog colonies averaged only 25 to 50% of that of undisturbed range. In South Dakota, Coppock et al. (1980, 1983b) found that peak live graminoid biomass in areas colonized for 1-2 years, 3-8 years, and > 25 years was 39, 61 and 97% lower, respectively, than in adjacent uncolonized areas. Coppock et al. (1983b) also found that standing dead biomass and litter (mulch) were increasingly reduced in colonies as time since colonization by prairie dogs increased. Archer et al. (1987) found that rapid changes occurred in the first 2 years following colonization, with bare ground increasing from 10 to 35% and litter cover decreasing from 20 to 10%.

High densities of prairie dogs may have a negative influence on native perennial grasses, may cause changes in plant species composition toward shorter grasses and, ultimately, toward annual and short-lived perennial forb species (Severe 1977, Coppock et al. 1983b, Lerwick 1974, Uresk 1984, Archer et al. 1987). Often buffalograss is the dominant plant on prairie dog colonies and the taller western wheatgrass and blue grama are most common on uncolonized mixed-grass prairie sites (Fagerstone et al. 1981, Agnew et al. 1986). In areas of greatest prairie dog activity, annual forbs, shrubs and cactus often replace most of the original grass cover (King 1955, Cincotta et al. 1989). Perennial grasses are rapidly displaced by annual forbs within 3 years of colonization by prairie dogs (Coppock et al. 1983b, Archer et al. 1987). Coppock et al. (1983b) found that



FIGURE 5. Large areas of bare ground are common in well established prairie dog colonies. Photo by K. Fagerstone.

graminoids accounted for 85% of the biomass on uncolonized grassland, 70% on a prairie dog colony colonized for 3 to 8 years, and <3% on a colony >26 years. The formation of forb dominated communities in prairie dog colonies has been attributed to the length of time since colonization and the level of prairie dog activity (Archer et al. 1987, Cincotta et al. 1989); forb domination is usually greatest in the center of the colony.

Forage improvement is very slow on western rangelands that have been heavily grazed for many years and researchers have speculated that total exclusion of herbivores (including cattle) for ≥ 9 years may be required to increase forage production when the range is in a low condition class (Uresk 1985). Uresk (1985) found that despite 4 years of black-tailed prairie dog removal, production of western wheatgrass did not increase. Buffalograss and needle leaf sedge (*Carex eleocharis*) showed significant decreases in production when cattle were allowed to graze after prairie dog removal, indicating that prairie dog clipping may have stimulated their growth.

Prairie dogs also can cause a shift in the proportion of C3 and C4 plant species (Fagerstone and Williams 1982). There are 2 main photosynthetic pathways used by higher plants: the C3 Calvin cycle and the C4 dicarboxylic acid pathway of photosynthetic CO_2 fixation. Caswell et al. (1973) found that C3 plants are generally nutritionally superior to C4 plants because the concentration of protein in C3 plants is highest in the leaf mesophyll cells, which are more easily broken down than leaf bundle sheath cells, where the concentration of protein is highest in C4 species (Caswell and Reed, 1975, 1976; Akin and Burdick 1977). In black-tailed prairie dog colonies, the percentage of C4 grasses and forbs in the habitat is higher than that predicted for typical short- or mixedgrass prairie (Caswell et al. 1973); the most likely explanation is that C4 species increase with heavy grazing pressure (Fagerstone and Williams 1982).

Prairie dog grazing can cause genetic changes within plant species (Detling and Painter 1983, Detling et al. 1986, Archer et al. 1987). Grasses consumed by prairie dogs contain higher silicon concentrations than those in uncolonized areas (Brizuela et al. 1984), which may make them more difficult to digest. The maximum height of some plant species on prairie dog colonies is also reduced (Detling and Painter 1983, Agnew et al. 1986, Archer et al. 1987), a reduction maintained even in the laboratory. In addition, plants from prairie dog colonies withstand defoliation by grazing better than plants from an ungrazed area, perhaps because those in colonies have a higher leaf blade/leaf sheath ratio and more horizontal leaf angles (Detling and Painter 1983).

Positive effects of prairie dogs on grassland productivity include greater soil aeration, changes in community structure, increased plant species diversity, greater forb production, and better quality food and growing conditions inside prairie dog colonies. Prairie dogs build burrows approximately 12 cm in diameter, 10–30 m long, and 1–5 m deep with 2 or 3 entrances (Sheets et al. 1971). Andelt (1984) and Sieg (1988) postulated that burrowing by prairie dogs decreases soil compaction, increases the intake of water, aerates the soil, and promotes soil formation. Soils in prairie dog colonies are richer in nitrogen,

phosphorus, and organic matter than soils in adjacent grasslands (Sieg 1988, Sharps and Uresk 1990).

On the southern Great Plains, prairie dogs can affect the structure and composition of rangeland in a positive manner by destroying mesquite (*Prosopis* spp.) seedlings before they can grow into nuisance shrubs. Weltzin et al. (1991) showed that honey mesquite (*Prosopis glandulosa*) seeds disappeared faster and seedling survival was lower on prairie dog colonies than off. They hypothesized that the eradication of prairie dogs may have allowed honey mesquite to increase in abundance over large areas of the Southwest.

Koford (1958) was one of the first to report greater numbers of plant species, primarily forbs, on prairie dog colonies than on native shortgrass prairie sites in Colorado. Since then, numerous other researchers have demonstrated an increase in plant species diversity in black-tailed prairie dog colonies in short- and mixedgrass prairie compared to uncolonized prairie (Lerwick 1974, Bonham and Lerwick 1976, Gold 1976, Hansen and Gold 1977, Severe 1977, Beckstead and Schitoskey 1980, Fagerstone 1982, Archer et al. 1984, Agnew et al. 1986, Archer et al. 1987). Also, forb cover can be significantly greater on prairie dog colonies (Uresk and Bjugstad 1983, Agnew 1983, Agnew et al. 1986).

Prairie dog grazing removes aging leaves and may stimulate growth of new tissue, which usually has a higher nitrogen concentration and greater digestibility than that of an ungrazed plant (McNaughton 1984). Prairie dog colonies, therefore, have been found to contain better quality food and growing conditions than uncolonized areas (Hassien 1976; Beckstead and Schitoskey 1980; Fagerstone 1982; Coppock et al. 1980, 1983b, 1983a; Detling and Painter 1983, Krueger 1986). Shoot nitrogen concentrations and digestibility are lowest in plants from uncolonized grasslands and increase with the length of time since colonization (Coppock et al. 1983b, Krueger 1986). Bison are attracted to prairie dog colonies as grazing sites (Coppock et al. 1983a) and use moderately grazed areas near the perimeters of prairie dog colonies because the vegetation contained higher crude protein and nitrogen levels, was more easily digestible, and had less dead matter (Coppock et al. 1983b).

Competition Between Prairie Dogs and Cattle. The economic effects of prairie dogs are not entirely clear. Although the black-tailed prairie dog diet is variable (Fagerstone 1982), the degree of dietary competition between prairie dogs and cattle can be high. The majority of plants eaten by prairie dogs are those also desired by livestock (Taylor and Loftfield 1924, Kelso 1939, Koford 1958, Fagerstone et al. 1981). Like cattle, black-tailed prairie dogs eat mainly grasses, followed by forbs and shrubs (Tileston and Lechleitner 1966, Summers and Linder 1978, Fagerstone et al. 1981, Uresk 1984). Similarity in diet between cattle and prairie dogs has been reported to be 64% by Hansen and Gold (1977) and 76% by Kelso (1939). However, prairie dogs feed selectively, so 80% of the biomass they ingest may come from plant parts not highly used by cattle (Crocker-Bedford 1976). Also, potential competition might be minimized by beneficial effects that large herbivores obtain from plants growing in prairie dog colonies because of increases in plant

digestibility and nitrogen content (Coppock et al. 1983b).

Control of black-tailed prairie dogs has long been considered necessary to increase forage production on rangelands and decrease competition with cattle for rangeland forage. Although experimental studies of competition between prairie dogs and steers failed to show that prairie dogs had a significant negative impact on weight of the steers (Hansen and Gold 1977, O'Meilia et al. 1982), the studies have demonstrated lower weight gains for steers raised on prairie dog colonies amounting to market values of \$14 to \$24 less/steer.

Eliminating prairie dogs has had little effect on increasing the amount of food available for cattle (Crocker-Bedford 1976, Klatt and Hein 1978, Collins et al. 1984, and Uresk 1985). The increase in livestock forage after prairie dog control in South Dakota was estimated at only 51 kg/ha/year; based on this gain, control of 7.2 ha of prairie dog colonies was required to gain 1 AUM (animal unit months) of grazing (Collins et al. 1984). At a prairie dog repopulation rate of 30%, the control was not economically feasible and annual maintenance costs were greater than the amount of forage gained. Controlling black-tailed prairie dogs on depleted rangelands in western South Dakota did not increase the amount of forage produced after 4 years, whether or not cattle were allowed to graze (Uresk 1985). Total exclusion from prairie dogs and livestock for between 4 and 10 years may therefore be required to increase forage production when the range is in a low condition class. In another study of prairie dog-cattle competition, O'Meilia et al. (1982) found no differences in forb production on pastures with steers only compared to pastures with steers and prairie dogs. However, they did find a significant reduction in availability of blue grama, sand dropseed (*Sporobolus cryptandrus*), and other grasses on pastures with prairie dogs.

Uresk and Paulson (1988) estimated the carrying capacity and forage utilization for cattle in western South Dakota when prairie dogs were present but pastures were maintained in good condition at a near climax stage of mixed perennial cool-season grasses. They found that carrying capacity for cows and for cow-calf units decreased as the number of ha occupied by prairie dog colonies increased; the decrease was approximately 3 AUMs or 2 cow-calf units for every additional 20 ha of prairie dogs. This study showed that when areas with prairie dogs were high, needle leaf sedge (*Carex eleocharis*) and needlegrasses (*Stipa* spp.) could become major limiting factors in determining cow carrying capacity. Western wheatgrass was never a limiting plant species because consumption never exceeded the amount available.

White-tailed Prairie Dogs

Historical populations. There are 3 species of prairie dogs generally grouped under the name "white-tailed prairie dogs" (Fig. 6). These 3 species are found mainly in mountain valleys and plateaus in the Rocky Mountains at higher elevations (1,830-3,660 m) than are black-tailed prairie dogs. Although white-tailed prairie dogs live in colonies, their social organization is loosely structured and more closely resembles that of ground squirrel aggregations than it does the more highly structured organization of black-tailed prairie dogs (Pizzimenti and

Hoffmann 1973). White-tailed prairie dogs occur at lower densities, (i.e., 3/ha) (Tileston and Lechleitner 1966, Clark 1977, Hoogland 1979) than black-tailed prairie dogs (approx. 15/ha) (King 1955, Koford 1958, Tileston and Lechleitner 1966, Hoogland 1979). White-tailed prairie dogs construct elaborate burrow systems and mounds; unlike black-tailed prairie dogs, white-tailed prairie dogs hibernate during winter. Habitat of white-tailed prairie dogs is variable and can contain densely vegetated areas, including sagebrush rangeland. As a consequence, visual contact between individuals is often obstructed, and alarm calls are important to the cohesion and survival of a colony (Waring 1970, Slobodchikoff and Coast 1980). Because white-tailed prairie dogs occur at lower densities and will tolerate more densely vegetated areas, they have generally not been considered as destructive to rangeland as black-tailed prairie dogs.

The white-tailed prairie dog has the largest geographic range of the 3 species and is found mainly in western Wyoming, northern Utah and northwestern Colorado (Fig. 7). Gunnison's or Zuni prairie dog occurs in Arizona, New Mexico, Utah, and Colorado (Slobodchikoff et al. 1988). The historical populations of these species are not well documented but Taylor and Loftfield (1924) reported that by 1924 heavy overgrazing by livestock caused the disappearance of tall grasses in the Southwest, possibly leading to increases in Gunnison's prairie dog populations over those existing before white men settled the area.

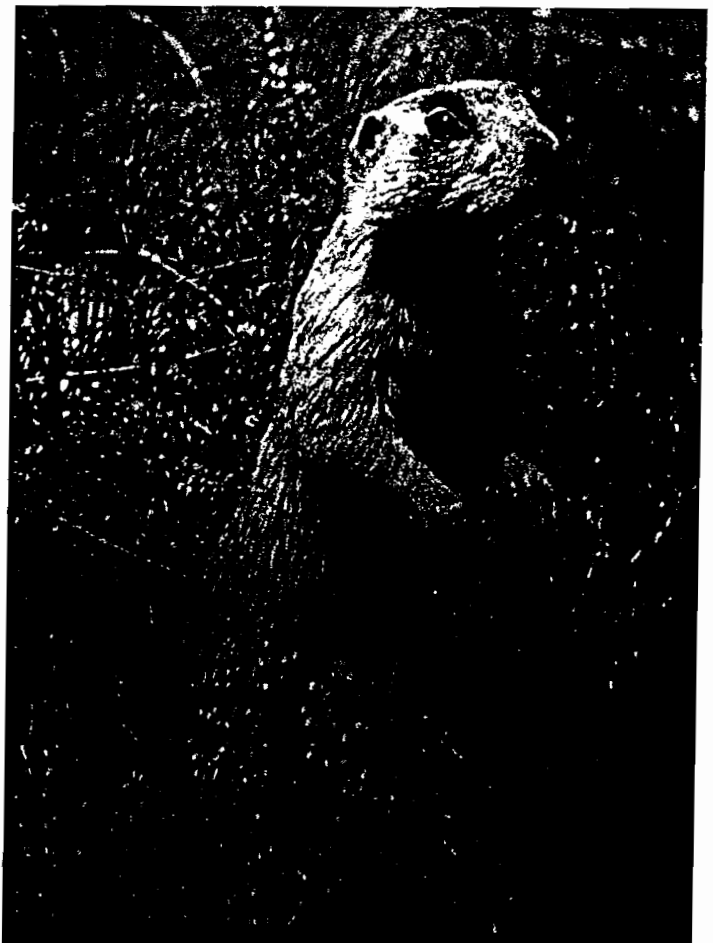


FIGURE 6. White-tailed prairie dog (*Cynomys leucurus*). Photo by K. Fagerstone.

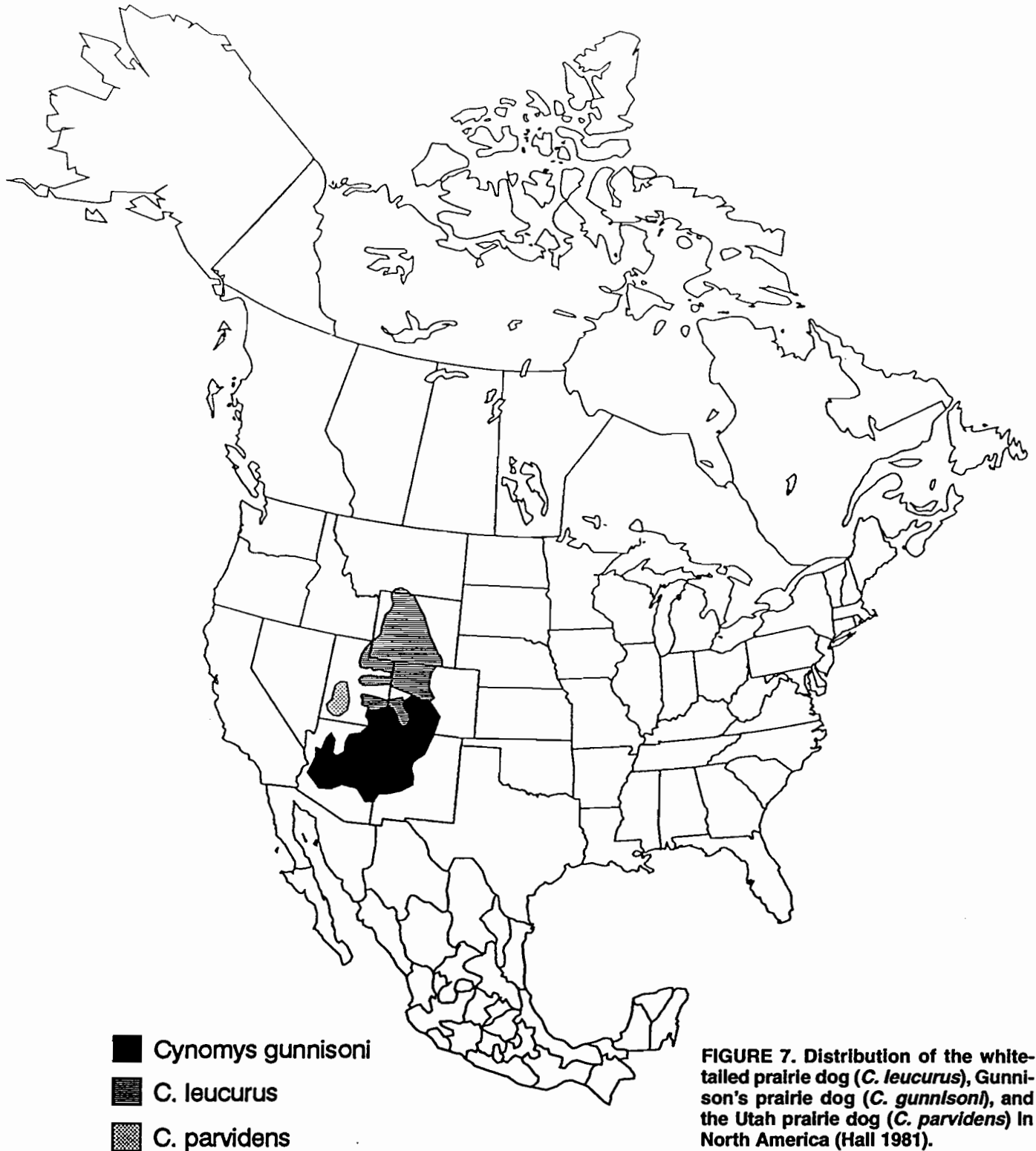


FIGURE 7. Distribution of the white-tailed prairie dog (*C. leucurus*), Gunnison's prairie dog (*C. gunnisoni*), and the Utah prairie dog (*C. parvidens*) in North America (Hall 1981).

The Utah prairie dog has the most restricted range of all the prairie dogs in the United States; it is found only in a few counties in southcentral and southwest Utah and is listed as an endangered species. After the 1920s its range constricted, until by 1975 it inhabited only half of its former range (Collier and Spillett 1975). Climate appears to be the single most important factor influencing the distribution of the Utah prairie dog, as population density has been correlated with the presence of

water and populations have disappeared or declined during periods of drought in the 1930s (Collier and Spillett 1975) and in the 1950's (Collier and Spillett 1972). Population numbers have been further reduced in the western portion of its range as a result of drying trends and invasion of shrubby vegetation.

Effects of Range Condition on White-tailed Prairie Dogs. Slobodkichoff et al. (1988) found that Gunnison's prairie dog density was highly correlated with the number of native species

in the area and was negatively correlated with the number of introduced-weedy plant species. They concluded that Gunnison's prairie dogs thrived at sites with native species of plants and did not prefer sites with a high proportion of introduced-weedy species. A study of prairie dog diet supported this conclusion, as 60-80% of the diet consisted of native plant species (Shalaway and Slobodchikoff 1988). Introduced weeds did not appear to be favored in Gunnison's prairie dog colonies, even though the soil was disturbed, suggesting that prairie dogs may cause some beneficial restoration of rangeland that has been damaged by grazing.

Gunnison's prairie dog density is positively correlated with the level of grazing (Slobodchikoff et al. 1988), suggesting that Gunnison's prairie dogs may prefer highly grazed sites. However, grazing has not been shown to play as large a role in promoting colony expansion of white-tailed prairie dogs as it does in black-tailed prairie dogs.

Effects of White-tailed Prairie Dogs on Rangeland. Little research has been conducted on the effects of white-tailed prairie dogs on grazing lands and uncertainty remains about their economic impact as competitors of livestock. Taylor and Loftfield (1924) found that destruction of vegetation and burrowing by Gunnison's prairie dogs accelerated sheet erosion, initiated gullies, and damaged primary forage species. A 4-year study on wheatgrass-dominated rangeland showed that Gunnison's prairie dogs utilized 80% of the total potential annual forage production. In blue grama-dominated rangeland, prairie dogs used 83% of the annual production. Gunnison's prairie dog fed on growing grasses and forbs in summer then switched to dead grass and seeds in spring and fall (Shalaway and Slobodchikoff 1988). Kelso (1939) found that plants of value as forage to livestock comprised 84% of the diet of the white-tailed and 75% of the diet of Gunnison's prairie dogs. However, white-tailed prairie dogs relied more heavily than the black-tailed on range plants that are not attractive to livestock, including sage (*Artemisia* spp.), saltbushes (*Atriplex* spp.), and Russian-thistle (*Salsola* spp.), which may offset competition with livestock.

In a Wyoming study, Clark (1977) found few vegetation differences between ungrazed rangeland and white-tailed prairie dog colonies ungrazed by livestock. However, where grazing by both prairie dogs and livestock occurred, grass height was reduced by half and forb abundance was doubled.

Gunnison's prairie dogs decreased plant cover (Slobodchikoff et al. 1988), an effect consistent with that found for black-tailed prairie dogs (Knowles 1982, Archer et al. 1984), but decreased plant species diversity (Slobodchikoff et al. 1988, Clements and Clements 1940), which is contrary to findings with black-tailed prairie dogs (Lerwick 1974, Bonham and Lerwick 1976, Gold 1976, Hansen and Gold 1977, Beckstead and Schitoskey 1980, Archer et al. 1984). The difference between plant diversity on black-tailed versus white-tailed prairie dog colonies is probably related to habitat differences associated with the 2 species. Black-tailed prairie dogs clip tall plants, promoting greater numbers of forb species, and increasing diversity. In contrast, white-tailed prairie dogs spend less time clipping forage, and the clipping action that occurs can lower the competitive ability of

shrubs, eventually eliminating them from prairie dog colonies and decreasing diversity. The decrease in plant species diversity and plant cover caused by prairie dog grazing apparently comes from a decrease in the introduced weedy plant species, and not from a decrease in native plant species.

Associations With Other Species

Through their modifications of aboveground vegetation, prairie dogs influence the densities, foraging patterns, and nutritional dynamics of other animals. Because these habitat modifications can be extensive, researchers refer to a "prairie dog ecosystem" that consists of the prairie dog community and other associated plants and animals.

Prairie Dog, Ungulate, and Rangeland Interactions. Many observers have reported that bison are attracted to grassland sites altered by prairie dogs (Koford 1958, McHugh 1958, Shult 1972) and suggest that prairie dogs and bison were ecologically fundamental to the functioning of the Great Plains grasslands prior to the coming of the white men (Coppock et al. 1983b, Krueger 1985). Koford (1958) suggested a reciprocal ecological relationship between prairie dogs and bison, each of which maintained a shortgrass interspersed with patches of forbs and bare ground, which was ideal habitat for the other. As bison moved into an area and denuded it of taller grasses, they increased visibility for prairie dogs, allowing prairie dogs to invade. Once established, prairie dogs kept their colonies open, which favored use by bison and antelope (*Antilocapra americana*). Coppock et al. (1983b) tested these theories and showed that bison actively selected prairie dog colonies over uncolonized grassland. One prairie dog colony was used 90% of the time by bison, even though the colony occupied only 39% of the habitat. Bison partitioned their use of the prairie dog colonies by preferentially resting in the oldest areas of prairie dog colonies (occupied for >26 years) and preferentially grazing in moderately affected areas of prairie dog colonies (occupied by prairie dogs for <8 years). Coppock et al. (1983a) found that bison selected for moderately grazed areas near the perimeters of prairie dog colonies; by continuously promoting new growth, prairie dogs modified plants in these areas toward more readily digestible perennial grasses, with lower fiber, higher nitrogen concentrations, and greater accessibility of green tissues, than vegetation from uncolonized areas. Despite the fact that maximum plant biomass occurred on uncolonized areas, bison used these areas least for grazing, perhaps because, as nonselective feeders, they cannot avoid feeding on standing dead vegetation, and prairie dog activities reduced the amount of dead vegetation. Thus, selection by bison for moderately affected sites in prairie dog colonies is a nutritionally advantageous tactic in a mixed-grass prairie. Vanderhye (1985) modeled the nutritional benefits accrued to bison by selectively feeding on prairie dog colonies and suggested that if bison use colonies for summer feeding, mature cows will gain an additional 5 kg of body weight (18% of seasonal weight gain) and yearlings will gain an additional 13 kg (46% of seasonal weight gain) compared to not feeding on colonies.

Elk (*Cervus elaphus*) (Wydeven and Dahlgren 1985) and pronghorn antelope (Krueger 1986) also preferentially use

prairie dog colonies for feeding. While bison are attracted to colonies to feed on the regrowth of grasses at colony edges, pronghorn antelope are attracted to the forbs in the core of the colony (Uresk and Bjugstad 1983, Coppock et al. 1983a, Knowles 1986, Krueger 1986, Detling and Whicker 1988).

Black-footed Ferret Interactions. Black-footed ferrets (*Mustela nigripes*) have a close association with prairie dogs (Henderson et al. 1969). Their original range corresponded closely to that of prairie dogs and they historically have been observed primarily on prairie dog colonies (Henderson et al. 1969, Hillman and Linder 1973, Campbell et al. 1987). Ferrets depend on prairie dogs for food (Hillman 1968, Fortenberry 1972, Sheets et al. 1972, Campbell et al. 1987), and are dependent on prairie dog burrow systems for denning sites and shelter. Therefore, their decline during this century is probably linked to the reduction in prairie dog numbers (Hillman 1968, Tietjen 1976) and possible secondary poisoning by strychnine and Compound 1080 as the result of eating poisoned animals (Rudd and Genelly 1956, Schitoskey 1975, Tietjen 1976). Although prairie dog populations have increased since 1972 when the use of secondary poisons on federal lands was banned, ferret populations have not increased concomitantly. The last known wild population was found in 1981 near Meeteetse, Wyoming, and was studied until 1985, when canine distemper, a disease fatal to ferrets (Carpenter et al. 1976), was diagnosed in the population following discovery of sylvatic plague (*Yersinia pestis*) in the white-tailed prairie dog colonies. The 18 ferret survivors were taken into captivity and a captive breeding program was begun that has increased their population to about 400 animals. Reintroduction to the wild was attempted during fall 1991 and 1992 in the Shirley Basin of Wyoming with limited survival of a few individuals. Further reintroductions are planned for Montana and South Dakota within 1 or 2 years, with the goal of developing 10 self-sustaining ferret populations. Currently, there are not enough large prairie dog populations to reach this goal so preservation of large prairie dog colonies will be essential for recovery of the black-footed ferret.

Interactions with Other Species. Prairie dog colonies provide a unique habitat that influences the abundance and species composition of birds, small mammals, and large herbivores. Prairie dog colonies provide habitat for many different species of vertebrates other than prairie dogs (Campbell and Clark 1981, Clark et al. 1982, O'Meilia et al. 1982, Agnew 1983). Clark et al. (1982) recorded 107 vertebrate species and subspecies of wildlife on prairie dog colonies in Utah, Colorado, and New Mexico. Sixty-four vertebrate species were recorded by Campbell and Clark (1981) on black- and white-tailed prairie dog colonies in Wyoming. Reading et al. (1989) listed 163 vertebrate species sighted on black-tailed prairie dog colonies and suggested that species richness increases with colony size and density. Sharps and Uresk (1990) determined that 134 species (40%) of western South Dakota wildlife were associated with prairie dog colonies. Agnew et al. (1986) and Deisch et al. (1989) found 5 classes of invertebrates on prairie dog colonies in South Dakota, which may explain why insectivorous rodent species are found in greater numbers on prairie dog colonies

than on surrounding rangeland (Agnew et al. 1988).

Prairie dogs serve as an important food source for mammalian predators. The black-footed ferret was historically an important predator, but currently the badger is the main prairie dog predator (Clark 1977). Others include coyotes (*Canis latrans*), bobcats (*Lynx rufus*), foxes (*Vulpes* spp.), and occasionally mink (*Mustela vison*) and long-tailed weasels (*Mustela frenata*) (Hillman and Sharps 1978). Swift fox (*Vulpes velox*) were normally found to have dens within 0.8 km of prairie dog colonies (Hillman and Sharps 1978) because prairie dogs are a major component of swift fox diet in South Dakota (Uresk and Sharps 1986).

Prairie dog burrows serve as homes for rabbits and rattlesnakes, whose numbers are usually higher on prairie dog colonies (Dano 1952, O'Meilia et al. 1982). On a grassland area in Colorado, desert cottontail (*Sylvilagus audubonii*) densities were 0.8 to 1.3/ha on prairie dog colonies and only 0.05 per ha on shortgrass prairie adjacent to the colonies (Hansen and Gold 1977). Colonies also provide habitat for a large number of small mammals. On mixed-grass sites in South Dakota and Oklahoma, small rodent abundance was found to be greater on than off black-tailed prairie dog colonies, but small rodent species richness was significantly lower (O'Meilia et al. 1982, Agnew et al. 1986). Prairie dogs act as ecosystem regulators by maintaining habitat with less mulch cover and lower vegetation height than surrounding ungrazed or lightly grazed rangeland. This vegetative manipulation by prairie dogs negatively impacts rodent species associated with dense vegetation of mixed-grass rangeland. However, these vegetation features, combined with high burrow densities, provide quality habitat for other species of small rodents, such as thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) (Evans and Holdenried 1943, Slade and Balph 1974), deer mice (*Peromyscus maniculatus*), and grasshopper mice (*Onychomys leucogaster*) (Agnew et al. 1986, Uresk 1987), which are associated with sparse, heterogeneous vegetative cover. Unused prairie dog burrows provide nesting and escape cover for these species (Koford 1958, Smith 1967). Maintenance of vegetation in a lower seral stage by prairie dogs is especially favorable to deer mice (Birch 1977), which are adapted to live in open habitat (Baker 1968, Jones et al. 1983, MacCracken et al. 1985a, Agnew et al. 1986). Their numbers decrease with increased vegetation height and canopy cover, so after prairie dog control with rodenticides, deer mice populations decrease (Uresk 1985, Deisch et al. 1990) as lack of clipping and grazing by prairie dogs causes increased plant canopy cover and above-ground biomass (Klatt 1971, Potter 1980). Because black-tailed prairie dog colonies contain large numbers of forbs, deer mice may be also be drawn to colonies to feed on seeds, their primary diet (Sieg et al. 1986). In prairie dog colonies an influx of deer mice usually occurs in spring when yearling deer mice establish home ranges (MacCracken et al. 1985a), and lower densities occur in August due to dispersal of young-of-the-year (Falls 1968, Metzgar 1980).

On white-tailed prairie dog colonies, where vegetation changes caused by prairie dogs are not as prominent, small

mammal populations were not found to differ between prairie dog colonies and uncolonized areas (K. A. Fagerstone, unpubl. data). Clark (1977) also found no differences in population densities of deer mice (about 40/ha), jackrabbits (*Lepus* spp.), and cottontail rabbits among ungrazed rangeland, rangeland grazed by white-tailed prairie dogs only, and rangeland grazed by prairie dogs and livestock. He trapped no ground squirrels on uncolonized areas or areas grazed by prairie dogs only. However, on the area grazed by prairie dogs and livestock, he found high densities (35/ha) of Richardson's ground squirrels (*Spermophilus richardsonii*) and 13-lined ground squirrels (30/ha). On heavily grazed rangeland, prairie dogs, Richardson's ground squirrels, and 13-lined ground squirrels will live together in a complex pattern of overlapping populations.

In a study of fauna associated with black-tailed prairie dog colonies, Agnew et al. (1986) found that bird species diversity and abundance were significantly higher on prairie dog colonies than on mixed-grass sites. They attributed the higher numbers to "patchiness" or structural diversity on prairie dog colonies, to increased forb seed production, and to lower amounts of mulch and lower vegetation height, which may result in greater visibility of macroarthropods and seeds. Species significantly more abundant on prairie dog colonies included horned larks (*Eremophila alpestris*), mourning doves (*Zenaidura macroura*), killdeer (*Charadrius vociferus*), barn swallows (*Hirundo rustica*), and burrowing owls (*Speotyto cunicularia*). The horned lark was the most common species and the shorter grasses on the colonies provided ideal conditions (Apa et al. 1991). Weins (1973) and Skinner (1975) found highest horned lark densities in grazed areas because the larks preferred open areas and low, sparse vegetation (Behle 1942, Skinner 1975) for optimum nesting habitat (DuBois 1935, Giezantanner 1970, Creighton 1974, and Pickwell 1931).

A large number of avian predators feed on prairie dogs, including golden eagles (*Aquila chrysaetos*), bald eagles (*Haliaeetus leucocephalus*), Ferruginous hawks (*Buteo regalis*), red-tailed hawks (*B. jamaicensis*), rough-legged hawks (*B. lagopus*), marsh hawks (*Circus cyaneus*), and other species (Clark 1977, Sharps and Uresk 1990). Burrowing owls use abandoned prairie dog burrows during spring and summer as nesting sites, for escape cover (O'Meilia et al. 1982, MacCracken et al. 1985b), and for feeding on the large numbers of insects and arthropods. The continued survival of the burrowing owl will probably depend on the presence of prairie dog colonies.

Prairie Dog Management Programs

It is important for land managers to recognize the positive and negative effects of prairie dogs on rangeland and on other wildlife species. Before developing a comprehensive management program, land managers should answer several questions. For example, what is the primary use of the rangeland: livestock grazing, wildlife value, or both? Are the prairie dog colonies of concern important for other wildlife species? What level of prairie dog occupation will be tolerated by landowners and the public? Is the rangeland in poor or good condition? And what is the purpose of the management plan: to increase, decrease, or

maintain current prairie dog colony sizes? Management strategies will differ depending on how these questions are answered.

Most research on prairie dog management has been conducted on black-tailed prairie dog colonies in South Dakota on mixed-grass climax rangelands. This research has focused almost exclusively on development of methods for reducing prairie dog populations and/or preventing increases in their numbers. Traditional techniques include shooting and toxicants. Intensive shooting of prairie dog colonies may successfully control their numbers by disrupting reproductive activities and removing individual animals (Andelt 1984). Toxicants that are legal for prairie dog control include poison grain baits and burrow fumigants (usually used for small areas). Zinc phosphide is a frequently used rodenticide for managing prairie dog colonies to decrease or maintain current colony sizes. Studies have shown that zinc phosphide can be effective in limiting colony expansion. Uresk and Schenbeck (1987) treated 7 colonies on 2 occasions over a 5-year period with zinc phosphide; 5 colonies were not treated. The untreated colonies increased 65% in area, while the treated colonies increased only 1%. They recommended treatment with a rodenticide every 3 years to curtail expansion of prairie dog colonies. Schenbeck (1982, 1986) obtained similar results, with most colonies needing retreatment at least once every 3 years to maintain a desired size.

If rangeland is in poor condition to begin with because of high intensity grazing by livestock and prairie dogs, it may take years after a prairie dog control program for range recovery to occur, even when livestock grazing is reduced. In South Dakota, >4 years of reduced prairie dog densities were needed for an increase in forage production (Uresk 1985). Based strictly on livestock forage response to rodenticide treatments, prairie dog control programs are not economically feasible (Uresk et al. 1982; Collins et al. 1984; Uresk 1985, 1986). Collins et al. (1984) reported that \$13.60/ha was spent on prairie dog control while grazing fees generated only \$7.30/ha per year. A serious problem with use of rodenticides to curtail colony expansion is the rapid recovery of prairie dog populations and the subsequent costs of frequent retreatments. Prairie dogs will frequently repopulate colonies to initial population numbers within 3 years (Schenbeck 1982, Cincotta et al. 1987).

Prairie dog management needs to be reexamined. Proper range management practices, such as reduction of livestock stocking rates and deferred grazing may be more effective than prairie dog control programs in regulating prairie dog numbers. Prairie dogs prefer habitat managed for warm-season grasses such as blue grama and buffalograss, a habitat favored by heavy livestock grazing (Uresk et al. 1982, Cincotta 1985). Prairie dog colony expansion can be reduced under management plans that use lower stocking rates to maintain a cool-season mid-grass rangeland rather than a short-grass rangeland; light grazing by livestock in mid-grass rangeland can result in greater height, cover, and density of vegetation (Uresk et al. 1982, Cincotta 1985), making habitat less suitable for prairie dog expansion. For example, prairie dog colonies did not significantly expand over 4 years on areas in South Dakota where cattle were excluded (Uresk et al. 1982). Snell and Hlavachick (1980) and

Snell (1985) also reported reduced expansion rates or elimination of prairie dog colonies by using a summer-deferred grazing system. In Nebraska rangeland, deferred grazing for 2 years caused a reduction in natality, population growth, and active areas (Cable and Timm 1988). Deferring a pasture from cattle grazing for 4 consecutive growing seasons reduced a 45-ha colony in southern Kansas by approximately 90% (Snell and Hlavachick 1980); summer grazing on the same colony was deferred again several years later when the colony began to expand, and after just 1 season of deferment, the colony decreased approximately 70% in size (Snell 1985). The average rainfall in the Kansas area was 63.5 cm, so vegetation responses and resulting prairie dog declines would be expected to be more dramatic than in drier areas of the Great Plains.

The most cost-effective control programs for managing prairie dogs to decrease or maintain current colony sizes may be those that combine the use of rodenticides with livestock grazing practices that reduce habitat suitability for prairie dogs by managing for taller grasses. This generally means periodic rest or reduced stocking rates of livestock (Uresk et al. 1982). Expansion and repopulation rates of prairie dog colonies can be controlled by reduced cattle stocking rates to increase height and density of vegetation in combination with rodenticide control programs and mechanical renovation of low quality rangeland (Snell and Hlavachick 1980, Schenbeck 1982, Uresk et al. 1982, Snell 1985).

Management to increase prairie dog colony sizes may become more prevalent in the future as more land managers recognize that prairie dog colonies are important and unique ecosystems. Management of prairie dogs for their positive values will undoubtedly be easier on public lands because private landowner attitudes towards black-tailed prairie dogs are often not favorable. Although many landowners will tolerate some prairie dogs, the 1980 South Dakota Litigation and the 1984 South Dakota weed and pest law are indicative of landowner attitudes in areas where prairie dog populations have been allowed to increase beyond the tolerance limits of local landowners and residents (Schenbeck 1986). In areas where prairie dogs are desired, a moderate level of livestock grazing may be required to enhance colony expansion.

New management techniques need to be developed that can be used in areas where rodenticide or fumigant treatments are not feasible and/or where grazing practices cannot be manipulated. One promising alternative is development of contraceptives that would place the management emphasis on reducing natality rather than on increasing mortality. Because prairie dogs reproduce only once a year, management efforts using immunocontraceptives would be minimal. Previous trials with diethylstilbestrol (DES) (i.e., a hormonal reproductive inhibitor) showed that limiting reproduction successfully limited expansion of a colony (Garrett and Franklin 1982); however, because DES accumulates in tissue and could affect reproduction on predators, it has not been pursued further. Because immunocontraceptives do not accumulate in tissue, they could be especially valuable in urban communities where prairie dog colonies have positive public value.

Less research has been conducted on management of white-tailed prairie dog populations. In areas overgrazed by cattle and prairie dogs, conditions similar to those in black-tailed prairie dog colonies may exist and grazing may need to be curtailed to prevent colony expansion. In other areas it may be beneficial to increase white-tailed prairie dog populations, particularly for the restoration of the endangered Utah prairie dog. Conservation of this species, and of Gunnison's prairie dog, may be enhanced by maintaining habitats with a large component of native vegetation (Slobodchikoff et al. 1988). Slobodchikoff et al. (1988) suggest that Gunnison's prairie dogs may have a beneficial function of promoting native vegetation that could help restore rangeland damaged by grazing.

Important questions still need to be addressed regarding prairie dog influences on rangelands. We know that grazing by prairie dogs decreases plant standing crop but we do not know to what extent that decrease may be offset by the increased nutritive value of the forage around prairie dog colony edges. We also know that a large number of animal species are associated with prairie dog colonies but we do not yet know which of those species are dependent on those colonies. Ideally, management of prairie dog colonies and rangeland should take into consideration a number of factors including range condition and trend, season of livestock use, prairie dog and livestock densities, how much area is available for colony expansion, and potential interactions with other species.

GROUND SQUIRRELS

There are 23 ground squirrel species (*Spermophilus* spp.) and a number of subspecies in North America (Hall 1981). Ground squirrels are distributed widely, with ≥ 1 species occurring throughout the Western United States. Ground squirrels range in length from about 17 to 52 cm (Fig. 8). Ground squirrels are active in the daytime and some species are social, forming sizable colonies ≥ 0.5 ha, with complex burrow systems. Ground squirrels feed on a wide variety of green herbage in late winter and spring and, in the more arid West, will often switch to a diet of seeds as green annuals disappear. Most ground squirrel species hibernate in winter; in the dry areas of the West they often have a summer torpor.

Preferred Habitat and Effects on Rangeland

Ground squirrels occupy widely varied habitats. Those species of most concern to rangeland managers primarily inhabit open grassy plains and valleys and generally avoid highly forested or brushy habitats. They are often less numerous where vegetation is tall and dense and their populations are therefore sometimes favored by livestock grazing.

Very little research has been conducted to quantify the effects of ground squirrels on rangeland. Ground squirrels can have positive effects on rangeland. Ground squirrel burrowing activities can contribute to deepening of soils (Grinnell 1923, 1933) by bringing subsoils to the surface where leaching, mixing, and distribution occur. Through their burrowing activities, ground squirrels also loosen the soil, admitting air and water to the roots

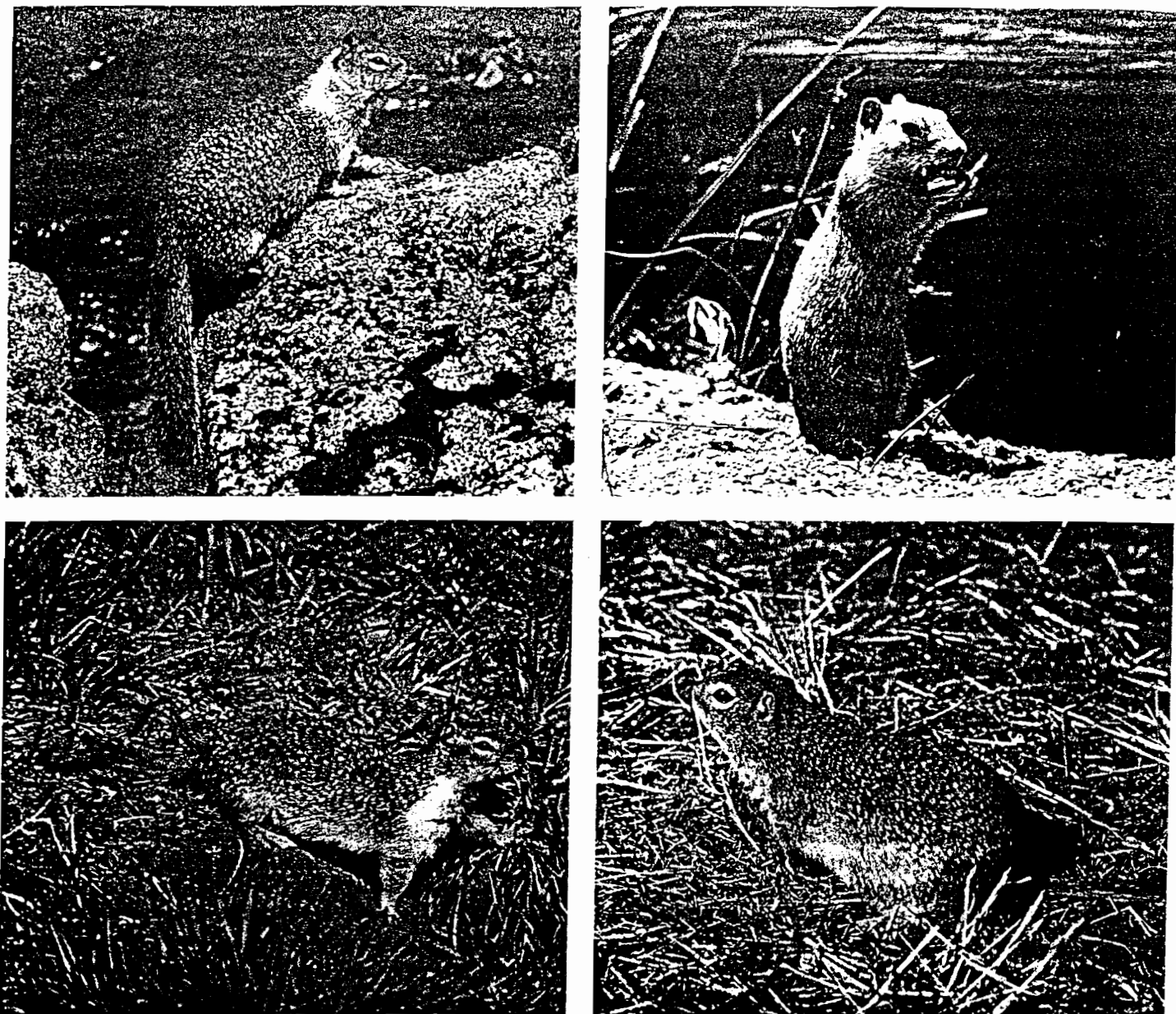


FIGURE 8. Several ground squirrel species influence rangeland vegetation, including: upper left, the California ground squirrel (*Spermophilus beecheyi*); upper right, Belding ground squirrel (*S. beldingi*); lower left, Columbian ground squirrel (*S. columbianus*); and lower right, Wyoming ground squirrel (*S. elegans*). Photos by K. Fagerstone, J. Clark, D. Sullivan, and K. Fagerstone, respectively.

of plants. It is estimated that 1 Columbian ground squirrel (*Spermophilus columbianus*) transports 4 to 12.3 kg of soil to the surface annually (Smith and Gardner 1985); newly constructed burrows result in the transfer of 25-50 kg of soil to the surface. Ground squirrel activities may prevent soil erosion by improving the water holding capacity of soil, thus producing greater vegetation cover (Grinnell 1923, Taylor 1935). Alternatively, on bare slopes they may increase erosion by depositing soil brought to the surface downhill from the burrow.

Several ground squirrel species are considered pests on rangelands, including the California ground squirrel (*Spermophilus beecheyi*), Belding's ground squirrel (*S. beldingi*), Richardson's ground squirrel, Wyoming ground squirrel (*S. elegans*), and the Columbian ground squirrel. There is controversy

about how much forage ground squirrels consume and the effect of this consumption on rangeland and livestock production. Many range managers contend that ground squirrels consume large quantities of range grasses and, therefore, conduct extensive control programs on rangelands. Although ground squirrels consume grasses that are important as livestock forage, little data have been generated on any species except the California ground squirrel to quantify the degree of conflict with livestock. For most ground squirrel species the primary conflict with man is consumption of cultivated crops rather than rangeland forage.

The California ground squirrel diet and effect on rangeland have been extensively studied. This species inhabits open areas of rangeland from sea level to 2,500 m (Grinnell and Dixon 1918). Populations are small on ranges protected from livestock

grazing (Linsdale 1946) and appear to benefit from the vegetation regrowth following disturbances created by grazing. The California ground squirrel has reportedly caused serious economic losses of forage production on livestock ranges in California (Calif. Dep. Agric. 1966). During the 1920s to the 1970s an average of 2.4 million ha/year were treated with poison grain to control ground squirrels, at a cost >\$1 million/year. The California ground squirrel competes with livestock primarily during the green forage season on California annual rangeland, where vegetation consists of annual forage plants that sprout from seeds in the fall following the first rains, and reach maturity in March, April, or May (Fitch and Bentley 1949, Howard et al. 1959). Ground squirrels can significantly reduce the amount of green forage available to grazing cattle during winter when plant growth is slow. Grinnell and Dixon (1918) estimated that 200 California ground squirrels would consume as much forage as 1 steer. Studies by Fitch (1948) and Fitch and Bentley (1949) indicated that California ground squirrels can consume a considerable amount of forage in spring; on the basis of an average population of 5.7/ha, they estimated that ground squirrels could consume about 12.4 kg of forage/ha/month. Estimates of the average daily intake of a California ground squirrel range from 20 to 49 g (Grinnell and Dixon 1918, Storer et al. 1944, Fitch 1948, Schitoskey 1978). In contrast to earlier studies, Schitoskey (1978) found forbs, including legumes, the most prevalent items in the diet, and suggested that during the green forage season California ground squirrels and cattle fed largely on different plant species. Schitoskey (1978) also found that intake varied with diet and sex; an adult male ground squirrel consumed 19.6 g of forage/day but only 16.3 g of dry seed/day; an adult female ate 15 g/day when nonreproductive, 19 g/day if pregnant, and 30 g/day if lactating. The ground squirrels could assimilate 83% of the dry matter in forage and 91% of the dry matter in seeds (Schitoskey 1978). This is similar to the 79.9 to 84.5% efficiencies reported for other rodents by Johnson and Groepper (1970) and Harris (1971). During the spring green forage season, ground squirrels feeding on foliage would require 1.5 times their daily energy needs to maintain their weight (Schitoskey 1978). Spring would therefore probably be the peak period of competition with livestock for rangeland forage. During summer and fall seed consumption, squirrels could eat less yet still gain weight, so competition is probably less intense.

Consumption does not wholly express the loss of forage due to ground squirrels because much is cut and left on the ground. California ground squirrels at densities of 4.9/ha reduced the forage by 35%, 10 times more than their forage consumption would indicate (Fitch and Bentley 1949). Howard et al. (1959) found that California ground squirrels can have measurable effects on livestock production. They compared winter weight gains of heifers on California ranges and found that where ground squirrels had been removed cattle weight gain was increased by 0.47 kg/day, equivalent to 2 kg of heifer weight for each ground squirrel removed. During the 2 years that ground squirrels were removed from an experimental pasture, heifers averaged daily gains of 0.5 and 0.3 kg greater than control animals in the pasture where squirrels were present. In contrast,

Schitoskey (1978) found that ground squirrels consumed only a small amount of net aboveground plant production.

The Belding's ground squirrel is plentiful on open grasslands of northwestern California and Oregon, southwestern Idaho, and Nevada. It avoids marshy areas and thick brush or rocky slopes but is not adapted to very dry conditions (Hansen 1954). According to Grinnell and Dixon (1918), extensive clearing of sagebrush and seeding to grass and hay benefited this squirrel, which feeds primarily on grasses. Grinnell and Dixon (1918) estimated that the forage eaten on a section of land densely populated with squirrels was sufficient to feed 90 steers throughout the growing season.

The Columbian ground squirrel inhabits wet meadows and grasslands from Montana and Idaho into Canada. Durrant and Hansen (1954) ranked the Columbian second to the Belding's as the ground squirrel least adapted to dry conditions. Density ranges from 12 to 35/ha on rangeland (Elliot and Flinders 1991), with the most densely populated areas situated on well-drained, south facing slopes (Boag and Murie 1981). Columbian ground squirrels eat a variety of rangeland flowers, seeds, bulbs, and fruits (Howell 1938, Manville 1959, Lambeth and Hironaka 1982, Elliot and Flinders 1985, Harestad 1986). The Columbian ground squirrel is considered to be one of the most economically harmful rodent species in western Montana, causing about \$800,000 damage in 1 year (Albert and Record 1982) to agricultural crops and rangeland. Much of the damage apparently arises from competition with livestock for forage (Shaw 1921, Fitch 1948, Howard et al. 1959), but good estimates are lacking. Shaw (1920) estimated that Columbian ground squirrels consumed 187% of their weight daily and that consumption by 385 Columbian ground squirrels would be equivalent to 1 cow and 96 to 1 sheep. Because of possible competition with livestock, this species has been the subject of intensive control efforts.

The Wyoming and Richardson's ground squirrels are very similar in habitat requirements, diet, and behavior and until recently were classified as 1 species (Fagerstone 1987). Both squirrels live in small social organizations similar to the clans described for the white-tailed prairie dog. The favored habitat of the Wyoming ground squirrel is well-drained upland slopes covered by dry grassland or sagebrush (Armstrong 1972; Clark 1970a,b; Hansen and Johnson 1976; Jones et al. 1983), where heavy clay soils, wet soils, and loose sand are avoided. Richardson's ground squirrels form large colonies in areas of short grasses and rough terrain, especially on heavily grazed slopes (Michener and Michener 1977, Michener 1979, Jones et al. 1983). Both species may be favored by overgrazing of rangeland. Sampson (1952) characterized the range where Wyoming ground squirrels occurred as having moderate to heavy grazing and being in fair to poor condition. He hypothesized that an increased population of squirrels may be a result of depleted range, where the squirrels subsist on secondary succession weedy plants. These squirrels primarily colonize low vegetation, rarely inhabiting sites where tall vegetation restricts their visual field (House 1964, Michener and Koeppl 1985). Hansen and Reed (1969) found that cattle and sheep grazing on their study area in late summer removed about 60% of the above-

ground plant biomass, which significantly reduced food for ground squirrels and induced competition for vetch (*Astragalus* spp.), bluegrasses (*Poa* spp.), and sandwort (*Arenaria* spp.). Therefore, although ground squirrels prefer the low vegetation of grazed areas, their populations may at times be adversely impacted in areas of intense livestock grazing.

Wyoming and Richardson's ground squirrels have been considered competitors to cattle on rangelands and reportedly do considerable damage when present at high population densities; however, damage has not been adequately assessed. Wyoming ground squirrels primarily eat green vegetation, with about 60% of their diet consisting of forbs and shrubs and 28% of grasses (Clark 1968, Hansen and Reed 1969, House 1964), so much of their diet consists of plants that are not particularly palatable to cattle. The diet and habitat requirements of Richardson's ground squirrels are similar to those of Wyoming ground squirrels; but Richardson's ground squirrels consume more grasses and fewer forbs and shrubs, so they may come into greater conflict with livestock. Leaves and stems of grasses, and a great variety of forbs, are consumed in spring and early summer, but in late summer and autumn, seeds are their principal foods (Quanstrom 1968). The average Wyoming ground squirrel has been estimated to remove about 1 kg/ha of aboveground vegetation each year, and the density of these squirrels may reach 50/ha (Hansen and Reed 1969). Average annual densities of adult Richardson's ground squirrels are between 1.4 and 5.2/ha (Dorrance 1974, Michener and Michener 1977, and Michener 1983) and on localized areas densities can be as high as 27/ha (Davis 1984); after emergence of young from burrows, Dorrance (1974) noted an average density of 10 juveniles/ha and a maximum of 56/ha.

Several other ground squirrel species are commonly found in association with rangeland but are not significant pests. In most of their range, Uinta ground squirrels (*S. armatus*) typically occur in open grassy meadows several successional stages removed from climax. They reach highest densities in gradually changing habitats (Slade and Balph 1974) and may be helped by moderate grazing. Thirteen-lined ground squirrels have been found to be most abundant in moderately overgrazed pastures, followed by heavily overgrazed and undisturbed areas (Phillips 1936). Jones et al. (1983) reported that thirteen-lined ground squirrels were most commonly found in short grass and Abramsky et al. (1979) typically found them in areas with open vegetation. However, Agnew et al. (1986) captured thirteen-lined ground squirrels most often in mixed-grass sites and only infrequently on shortgrass areas such as prairie dog colonies. Townsend ground squirrel (*S. townsendii*) diets were the same on grazed and ungrazed habitats (Rogers and Gano 1980), not surprising because these ground squirrels are active above ground only during late winter and spring when green plant material is readily available. They remain below ground in a torpid condition the rest of the year when green forage is scarce, thereby precluding intense competition with livestock. Washington's ground squirrels (*S. washingtoni*) inhabit dry, open sagebrush or grassland habitat but are most numerous in areas of high grass cover (Betts 1990), where population densities may range from 120 to 240 individuals/ha (Bailey 1936, Dalquest 1948).

Management

Management for most species of ground squirrels has emphasized population reduction. Various rodenticides are effective for reducing ground squirrel populations, including sodium fluoroacetate and strychnine (no longer available for this use), zinc phosphide, chlorophacinone and diphacinone, bromadiolone and gas cartridges (Record 1978, Albert and Record 1982, Askham 1985, Matschke et al. 1988). Chemical toxicants distributed on grains can result in immediate mortality >70% (Record 1978, Matschke et al. 1983). Generally, however, post-treatment reinvasion by squirrels from surrounding areas rapidly returns populations to pretreatment levels.

Given the paucity of quantitative studies on the effects of ground squirrels on rangeland and livestock, rangeland managers should evaluate carefully before ground squirrel control is undertaken. Ground squirrels have many positive roles in the grassland ecosystem, particularly as an important prey base. Predators of ground squirrels include canids (coyotes and fox), felids (bobcat [*Lynx canadensis*], and mountain lion [*Felis concolor*]), bear (*Ursus* spp.), mustelids (badgers [*Taxidea taxus*], weasels [*Mustela* spp.], marten [*Martes americana*], and skunk [*Mephitis* spp.]), buteos (red-tailed hawks, Ferruginous hawks, and Swainson's hawks [*B. swainsoni*]), marsh hawk, prairie falcon (*Falco mexicanus*), eagles, owls (snowy owl [*Nyctea scandiaca*], and great horned owl [*Bubo virginianus*]), and black-billed magpies (*Pica pica*) (Michener 1979, Michener and Koepl 1985, Elliot and Flinders 1991). Domestic cats and dogs also hunt ground squirrels. Long-tailed weasels, badgers, and buteos probably have the greatest impact on ground squirrel populations. Michener (1979) found that predation by long-tailed weasels on unweaned young in the burrow reduced the number of juveniles entering the population > 50%. Ground squirrels are most vulnerable to predation from badgers during fall after squirrels enter hibernation but before the ground is frozen, so badgers can dig them out of burrows (Michener 1979). Ground squirrels can be a very important source of food for predators. During the nestling period for buteos in southern Alberta, Richardson's ground squirrel averaged 90% of the prey biomass for ferruginous hawks, 76% for red-tailed hawks, and 75% for Swainson's hawks (Schmutz et al. 1980). Buteos killed 6% and 15% of the squirrel population in 2 different years.

POCKET GOPHERS

Pocket gophers are fossorial rodents in the family Geomyidae. They are medium-sized, with lengths ranging from about 12.5 to 35.5 cm and color ranging from dark brown to almost white. The great variability in size and color is attributed to a low dispersal rate and limited gene flow that results in adaptation to local conditions. Pocket gophers are found throughout most rangelands in the United States but they are seldom seen, spending most of their lives underground in burrow systems that provide shelter and access to forage. Their many adaptations for life underground include small eyes, inconspicuous ears, powerful forequarters, long claws and incisors for digging, and specialized lips behind the front teeth to prevent soil from enter-

ing the mouth. Pocket gophers were named for the large pouches on either side of the face that are used for carrying food. Gophers are active all year round. Usually only 1 gopher occupies a tunnel system except during the breeding season and when females are rearing young. In northern localities pocket gophers have 1 litter/year, usually with 3 to 4 young but in southern areas they may have ≥ 2 litters depending on the locality and climate.

There are 33 species of pocket gophers represented by 5 genera in the western hemisphere (Hall 1981). The 2 primary genera of pocket gophers are *Geomys* and *Thomomys*. *Geomys* are present from the Rocky Mountains east to the Mississippi River, and from southern Canada to southern Texas. The 3 main *Geomys* species in North America are the plains pocket gopher (*Geomys bursarius*) (Fig. 9), the desert pocket gopher (*G. arenarius*), and the Texas pocket gopher (*G. personatus*). The plains pocket gopher is the most widespread (Fig. 10). Adults average about 31 cm in length and weigh 250–450 g and can occur at densities as high as 20/ha.

Thomomys species occur generally in the western states (Hall 1981). The northern pocket gopher (*T. talpoides*) (Fig. 11) is widely distributed from Canada south to northern California and New Mexico, and from the west coast east to the Dakotas (Fig. 12). It is typically 16.5 to 25 cm long with yellowish-brown fur. The southern pocket gopher (*T. umbrinus*) is found from Mexico into southern Oregon and east into Colorado and is slightly larger (13 to 34 cm long) with fur that varies from almost white to black. The other species of *Thomomys* have more limited distribution. Densities are highly variable and may range from 7.5 to 96 animals/ha (Richens 1965, Reid et al. 1966), probably averaging 45/ha.

Pocket gopher burrow systems consist of runways usually 10 to 60 cm underground running generally parallel to the surface. Side tunnels off the main runways are used as exits from the system and for deposition of soil, debris, excess food, and feces. Deeper tunnels, at 1.5 to 3 m, lead to nests and food caches. Tunnels are not open to the surface and gophers will generally plug any openings in the tunnel system within 24 hours. A gopher makes characteristic mounds of soil when digging its

tunnel and pushing loosened soil out the tunnel to the surface (Fig. 13). The tunnel system of a single gopher may average 35 to 50 m in length for *Geomys* spp. (Thorne and Andersen 1990, Stubbendieck et al. 1979) and 1 gopher may build 100 mounds and move 1.8 metric tons of soil to the surface in a single year (Stubbendieck et al. 1979). Tunnel systems may range from 25 to 63 m in length for *Thomomys* spp. (Smith 1948, Turner et al. 1973) and occupy about 185 m² (Turner et al. 1973). Andersen (1987) and Thorne and Andersen (1990) showed that as much as 69% of the tunnel length excavated was later backfilled, indicating that underground excavation exceeded the amount visible from the surface. During winter, pocket gophers may burrow just under the snow, leaving characteristic castings of soil on top of the ground after the snow melts (Fig. 14).

Preferred Habitat and Impact of Grazing on Pocket Gophers

Pocket gophers occupy coastal areas to elevations of 3,600 m. They are found in a variety of soil types but reach their highest densities on loose, lightly textured soils with good drainage and high porosity (Davis et al. 1938, Kennerly 1964, Miller 1964, McNab 1966, Turner et al. 1973). Because their tunnels are closed, pocket gophers depend upon diffusion through the soil into the tunnel for gas exchange that is facilitated by light textured, porous soils with good drainage. Wet soils or soils with high clay content diffuse gases poorly and are unsuitable for gophers (Kennerly 1964, McNab 1966). The plains pocket gopher is usually restricted to deep sandy and silty soils (Miller 1964, Turner et al. 1973). Downhower and Hall (1966) found that plains pocket gophers in Kansas occurred only in soils with clay content < 30% and sand content > 40%. In Colorado, they are common in alfalfa (*Medicago sativa*) fields, sandhill rangelands, and river bottoms, but are not abundant in shortgrass prairie or areas with compacted soils (Turner et al. 1973). Beck and Hansen (1966) found plains pocket gophers in eastern Colorado to be more abundant on sandy loam soil compared to dune sand, possibly because of greater abundance of plants used for food on the sandy loam soils. The Mexican pocket gopher (*Pappogeomys castanops*) is a large pocket gopher species (occurring primarily in New Mexico and Texas) that prefers soil conditions similar to the plains pocket gopher but has a broader soil tolerance (Miller 1964, Moulton et al. 1983).

Thomomys species generally have a wider soil tolerance. The valley pocket gopher (*Thomomys bottae*) is a small animal that can live in a wider range of soil types than *Geomys* spp. (Miller 1964). Northern pocket gophers have the widest tolerance, occurring in soils ranging from deep sandy soils of the plains to shallow gravel in mountainous areas (Miller 1964, Hansen and Morris 1968). Local distribution of all pocket gophers can be determined by soil depth (Davis et al. 1938), as they require soils > 10 cm deep for their burrows, possibly to prevent cave-ins and exposure to extreme temperatures during mid-summer and winter (Howard and Childs 1959, Kennerly 1964, McNab 1966). Pocket gophers live successfully in soils where mean soil moisture ranges from < 10% to > 50% (Hansen and Beck 1968) but are not found in continuously wet soils. Ingles (1949)

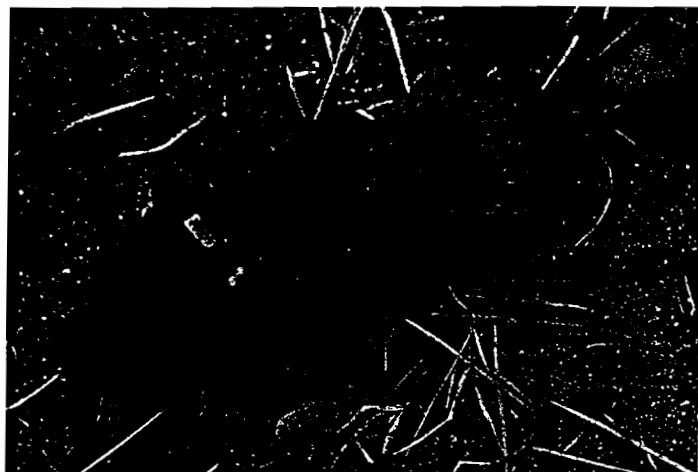


FIGURE 9. Plains pocket gopher (*Geomys bursarius*) equipped with a radiotelemetry collar. Photo by K. Fagerstone.

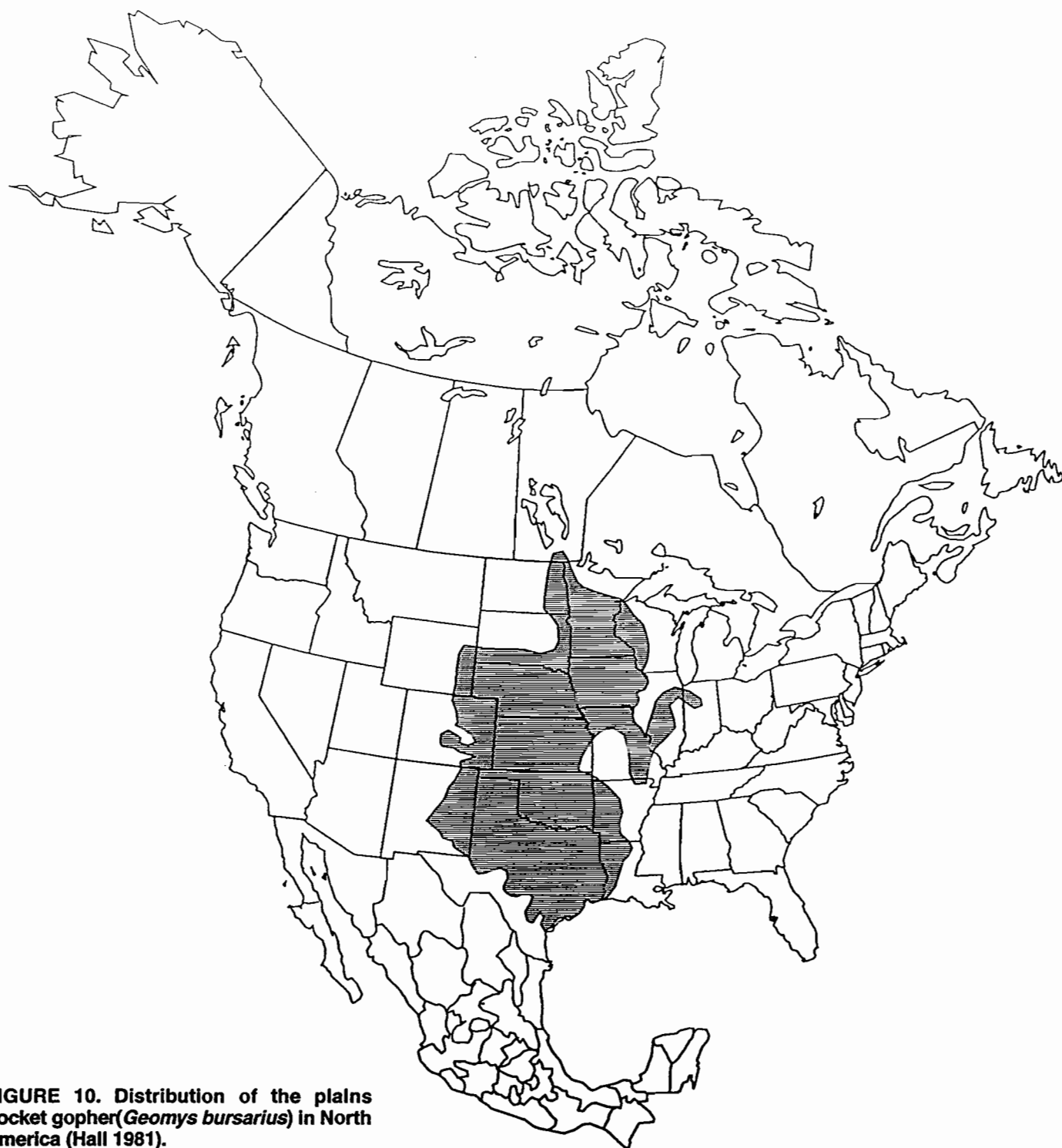


FIGURE 10. Distribution of the plains pocket gopher (*Geomys bursarius*) in North America (Hall 1981).

described how a rising groundwater table forced a local population to vacate suitable habitat.

Pocket gophers are attracted to rangeland in good to excellent range condition, where they use vigorous plants with large root systems. Pocket gopher densities appear to be dependent on plant biomass (Keith et al. 1959, Downhower and Hall 1966, Andersen and MacMahon 1981), particularly biomass of dicotyledonous plants (Williams and Cameron 1990). Tilman (1983) and Reichman and Smith (1985) found that gophers inhabited portions of fields with the highest biomass. Lower

plant biomass may require gophers to burrow more extensively to locate food, a theory supported by Reichman et al. (1982). They found that pocket gopher burrows were only half as long in areas with twice the plant biomass. Vleck (1981) observed that once a gopher encountered a resource patch, it exploited that patch rather than constructing additional burrows. Spencer et al. (1985) postulated that on a burned area pocket gopher foraging movement increased in response to the concomitant decrease in forb biomass; similar increases in foraging were not observed on an unburned area.

Grazing has often been alleged to favor large pocket gopher populations (Buechner 1942). However, the impact of grazing on pocket gophers actually appears variable. In 2 studies of northern pocket gopher populations, no significant differences were found among mountain ranges grazed or ungrazed by cattle (Turner 1969, Turner et al. 1973). Other studies have shown higher pocket gopher numbers on ungrazed areas. Moore and Reid (1951) and Ellison and Aldous (1952) found that gophers tended to concentrate inside ungrazed livestock exclosures, and Hansen (1965), Turner et al. (1973), and Hunter (1991) found lower densities of southern pocket gophers and northern pocket gophers in grazed areas. Turner et al. (1973) found a mean of 9 northern pocket gophers/ha on ungrazed ranges compared to only 2/ha on ranges that were grazed lightly, moderately, and heavily by cattle. On Grand Mesa, Colorado, mounds and castings covered 5% more ground surface, and occurred 14% more frequently, on ranges where cattle had been excluded 10 years than on adjacent moderately grazed ranges (Turner 1969). However, other comparisons involving grazing intensity have shown heavily grazed range to have higher gopher densities than lightly grazed range (Laycock 1953). Although these results seem contradictory they may have a biological basis. During the summer grazing season, both sheep and cattle consume large quantities of forbs, which are also the preferred summer foods of northern pocket gophers. Forb availability may be highest for gophers on ungrazed range versus lightly or moderately grazed range and may allow for higher pocket gopher densities on the ungrazed areas. On the other hand, higher pocket gopher densities on heavily grazed range may be an effect of long-term heavy grazing, which can promote greater abundance of forb species than moderate or light grazing.

In contrast to the northern pocket gophers, plains pocket gophers are reported to be most abundant on moderately grazed range, less abundant on ungrazed or lightly grazed range, and absent or least abundant on heavily grazed range (Phillips 1936, Colorado Cooperative Pocket Gopher Project 1960). They seem to prefer the varied vegetation of disturbed grasslands and are more abundant in these areas, provided the soil is suitable for burrowing.

Effect on Rangeland

Pocket gophers affect rangeland in a variety of ways: by burying plants; by transporting nutrients to the soil surface during burrowing and mound formation activities; and by feeding, which decreases biomass of forage plants and alters plant species composition. Pocket gophers compete directly with livestock by consuming range plants, above and below ground. The major food plants of northern pocket gophers are also major food plants of cattle on the same range (Ward and Keith 1962). Consumption of forage by gophers is much higher than for other small mammals because of the higher energetic demands of burrowing (Andersen and MacMahon 1981, Gettinger 1984). Where pocket gophers occur in abundance, they may be the primary non-ungulate consumer of forage, frequently harvesting more vegetation than they actually eat and storing it in underground food caches. Pocket gophers consume primarily belowground

vegetation but eat aboveground vegetation during periods when the vegetation is green and succulent (Miller 1964, Andersen and MacMahon 1981, Williams and Cameron 1986b).

Although the pocket gopher genera are much alike anatomically and have similar ecological roles, they differ considerably in their diets and in their abilities to use certain foods (Myers and Vaughan 1964). Forbs comprise a much larger portion of the northern pocket gopher diet (67-93%) (Keith et al. 1959, Ward and Keith 1962, Turner et al. 1973, Vaughan 1967) than of the plains pocket gopher diet (30%) (Myers and Vaughan 1964). Keith et al. (1959), Ward (1960), Ward and Keith (1962), and Vaughan (1967) found that forbs are preferred and grasses are a low preference food for northern pocket gophers. Keith et al. (1959) studied the effect of spraying mountain rangeland with 2,4-D. Forb cover was sharply reduced, from 67% of the vegetation and 82% of the pocket gopher diet before spraying to only 30% of the vegetation and 50% of the diet after spraying. Pocket gopher numbers dropped 87% following the spraying because of an apparent inability to survive where forbs were eliminated (Tietjen et al. 1967). Laboratory feeding tests by Tietjen et al. (1967) further demonstrated this inability to survive on a diet high in grasses; only succulent grasses or those bearing corms or rhizomes yielded a subsistence diet, and pocket gophers lost weight even on those grasses. These studies suggest that the optimum habitat for northern pocket gophers is high in forbs.

In contrast to *Thomomys* species, *Geomys* species frequently thrive in grassland areas with few forbs. Myers and Vaughan (1964) studied a population of plains pocket gophers on sandhill rangeland in Nebraska where the summer vegetation was 99% grasses, and the summer diet was 77% grasses, with 6 of 10 preferred plants being grasses. Although grasses constitute the bulk of the diet of plains pocket gophers (Myers and Vaughan 1964, Foster and Stubbendieck 1980, Tilman 1983, Williams and Cameron 1986b) and Mexican pocket gophers (Hegdal et al. 1965), succulent forbs are used when available and may be important to pocket gopher survival, as plains pocket gophers feed on some forbs in higher percentages than forbs appear in the habitat. In eastern Colorado, 88% of the vegetation was grasses, but grasses comprised only 64% of the gopher's yearly

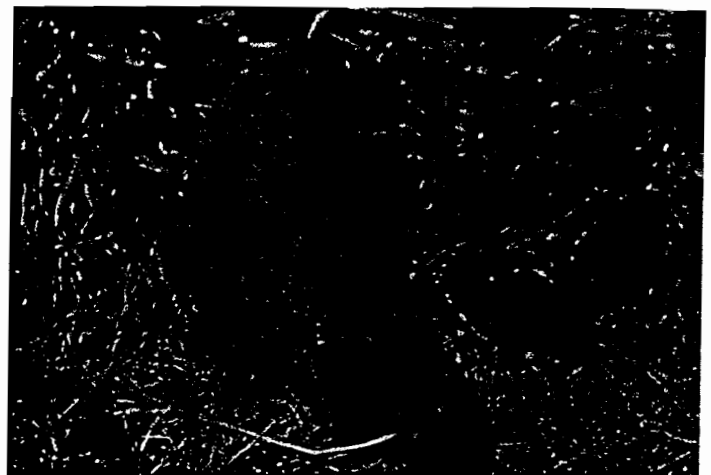


FIGURE 11. Northern pocket gopher (*Thomomys talpoides*). Photo from the Denver Wildlife Research Center Archives.

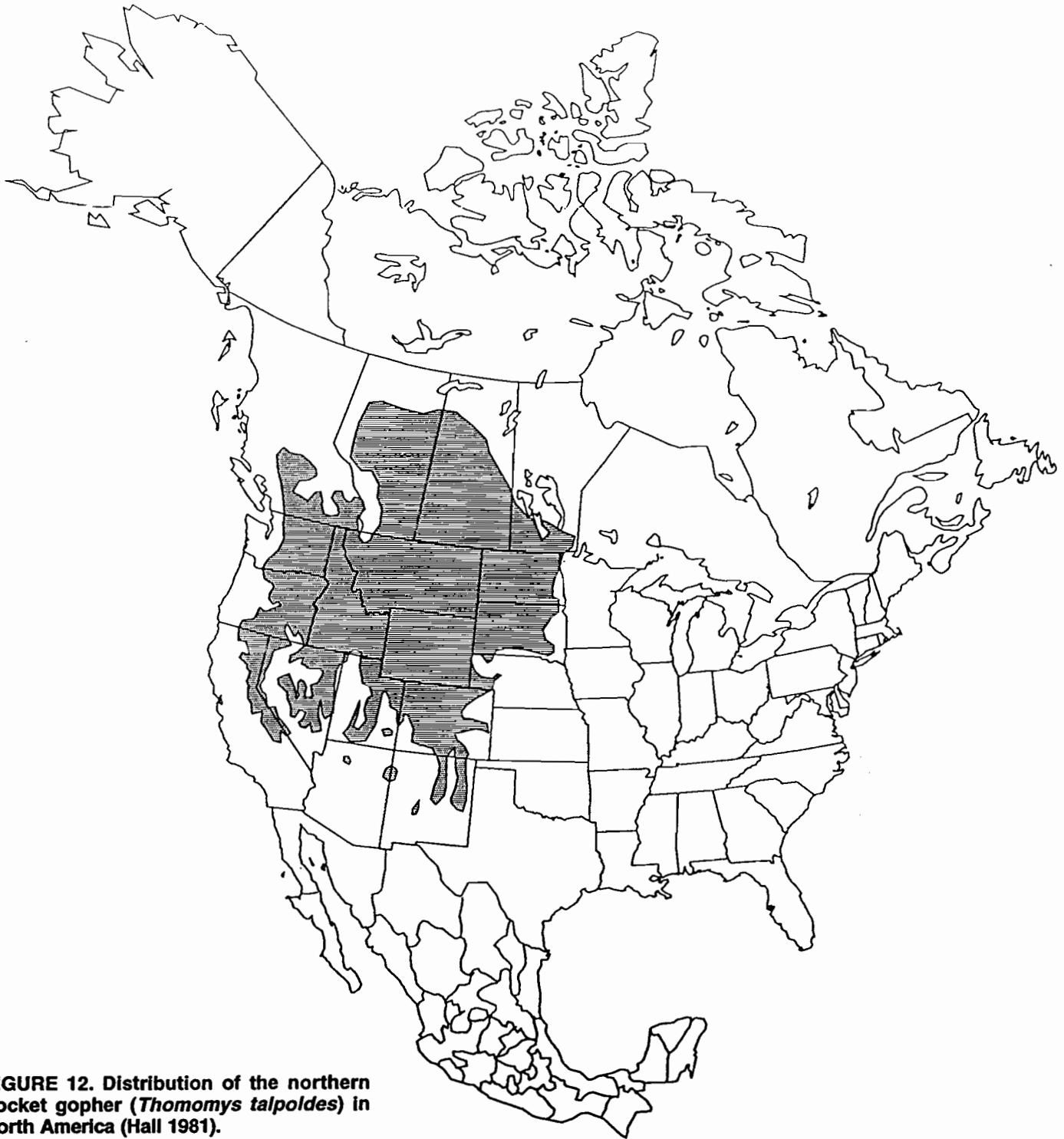


FIGURE 12. Distribution of the northern pocket gopher (*Thomomys talpoides*) in North America (Hall 1981).

diet (Myers and Vaughan 1964). Luce et al. (1980) found that grasses comprised 98% of the vegetation but only 45% of the diet, with forbs comprising 10% and a rush species 15%.

Plains pocket gophers can decrease the forage availability of some desirable livestock grasses on rangeland by their feeding habits. Sand bluestem (*Andropogon hallii*), prairie sandreed (*Calamovilfa longifolia*), needle and thread (*Stipa comata*), western wheatgrass, and blue grama are highly preferred foods for pocket gophers (Myers and Vaughan 1964, Luce et al. 1980). However, not all forage eaten by pocket gophers is of value to

livestock; some species of poor forage value to livestock are eaten in small quantities by pocket gophers, including western ragweed (*Ambrosia psilostachya*), thistles (*Cirsium* spp.), and cactus species.

Several studies demonstrated pocket gophers can decrease forage production on rangeland by consumption, clipping, burying litter and vegetation, and reducing plant vigor. However, the amount of the decrease in production varies between short-grass and tall-grass sites and between range condition classes within sites (Stubbendieck et al. 1979, Foster and Stubbendieck 1980,



FIGURE 13. Characteristic mounds of soil made by pocket gophers as they dig tunnels and push soil to the surface. Photo by K. Fagerstone.



FIGURE 14. Soil casts formed by pocket gophers in winter when soil from below ground is pushed into snow tunnels. When the snow melts the soil (tubes) remain on the ground. Photo by K. Fagerstone.

Williams and Cameron 1986a). Plains pocket gophers have been shown to have a significant impact on forage production on western Nebraska rangelands, decreasing overall production by 18-49% (Foster 1977, Foster and Stubbendieck 1980) and reducing plant biomass directly over burrows by one-third (Reichman and Smith 1985). In Texas, biomass increased 22% when plains pocket gophers were excluded from rangeland (Williams and Cameron 1986a). Fitch and Bentley (1949) observed that southern pocket gophers at a density of 79/ha reduced annual forage production 25% (destroying 284 kg/ha during the growing season) on foothill rangelands in California, where the plant composition was predominantly annual plants. They concluded that pocket gophers had a greater effect on vegetation than ground squirrels and kangaroo rats (*Dipodomys* spp.). Northern pocket gophers reduced herbage production about 20% (224 kg/ha) on mountain rangeland in Colorado (Turner 1969) and 30% in an alpine meadow (Andersen and MacMahon 1981). Alsager (1977) found that forage yields on rangelands in southwestern Alberta, Canada, increased 16% where northern pocket gophers were controlled compared to yields on areas without control. In Utah, following partial control of pocket gophers for 1 to 4 years, herbage production exceeded that on a nearby area on which gophers were not controlled by 560 to 672 kg/ha (Richens 1965).

In addition to changing forage availability, pocket gophers can alter the vegetation species composition of rangeland by feeding upon and burying herbage, and by altering the microenvironment (Branson and Payne 1958, Turner 1969, Turner et al. 1973, Laycock and Richardson 1975, Tilman 1983). Plant species eaten by gophers tend to decrease on rangeland while unpalatable species increase (Myers and Vaughan 1964). Pocket gopher feeding and burrowing activity promotes the presence of annual grasses, annual forbs, and perennial forbs, while decreasing the frequency of perennial grasses (Turner et al. 1973, Foster and Stubbendieck 1980, Kjar and Stubbendieck 1980, Martinsen 1989). These changes in plant composition are

related to precipitation, with the most severe changes occurring in areas receiving low precipitation amounts (Kjar and Stubbendieck 1980). Turner et al. (1973) found that pocket gophers caused major changes in vegetation composition on high mountain rangelands, suppressing productivity of some livestock forage species such as common dandelion (*Taraxacum officinale*), lupine (*Lupinus* spp.), agoseris (*Agoseris glauca*), and aspen peavine (*Lathyrus leucanthus*), and increasing production of orange sneezeweed (*Helenium hoopesi*), which is poisonous to sheep and unpalatable to cattle. Two grass species palatable to livestock, slender wheatgrass (*Agropyron pauciflorum*) and mountain brome (*Bromus carinatus*), also benefited from gopher activity. Luce et al. (1980) measured differences in vegetation on rangeland occupied by plains pocket gophers versus unoccupied rangeland and found major changes in basal cover of prairie sandreed and blue grama. Prairie sandreed comprised 25.4% of the basal cover of the vegetation on unoccupied rangeland versus 5.2% on the occupied area; blue grama comprised 16% of basal cover in the unoccupied area and only 7% in the occupied area. A decline in range condition often follows after occupation by pocket gophers as the desirable perennial grasses rapidly decline, accompanied by an increase in annual grass and forbs. This decline may cause gophers to move into previously unoccupied areas and abandon the now weedy areas.

Pocket gopher digging activity can result in decreased biomass and increased bare soil and litter on occupied rangeland. Much of this digging occurs in late summer and fall when young gophers establish their own burrow systems and when adults burrow extensively in search of underground food. However, digging and consequent burial of plants occurs even after snowfall as pocket gophers burrow under the snow. Pocket gopher mounds commonly cover 5 to 15% of the soil surface, with values reported up to 25% (Turner et al. 1973, Stubbendieck et al. 1979, Grant et al. 1980, Spencer et al. 1985) (Fig. 15). Spencer et al. (1985) found that new mounds were formed at the rate of about 58/ha/day on a Texas prairie. Estimates vary regarding



FIGURE 15. Pocket gopher mounds can cover up to 25% of the ground surface in areas of high animal density. Photo by K. Fagerstone.

the amount of soil brought to the surface by pocket gophers. Downhower and Hall (1966) estimated that 1 plains pocket gopher may bring 4,483 kg of soil to the surface annually. The amount of soil brought to the surface each year by *Geomys* spp. in Texas has been estimated at 15,690 kg/ha by Buechner (1942) and between 84,000 and 103,000 kg/ha by Spencer et al. (1985). Gophers in Texas prairie deposited enough soil to cover the entire area in 4 years if no area was covered more than once (Spencer et al. 1985). Estimates for *Thomomys* spp. vary from 11,250 kg (Ellison 1946, Grant et al. 1980) to 85,200 kg (Richens 1966) of soil/ha/year. The deposited soil may bury vegetation and prevent growth of the underlying vegetation (Ellison 1946, Moore and Reid 1951). Plant succession on denuded areas may be slow and may continually provide colonization sites for early successional species (Laycock 1958), many of which are undesirable as livestock forage. Ellison (1946) found that gopher mounds made poor seed beds and Laycock (1953) showed that few plants appeared on northern pocket gopher mounds the season mounds were made; the first plants to appear were usually annuals (Laycock 1958), followed by perennial dicots (Martinsen 1989). Williams et al. (1986) and Martinsen (1989) observed that herbaceous perennial dicots benefit from pocket gopher disturbance by germinating and surviving on mounds in greater numbers than off mounds. Vegetation density on pocket gopher mounds increases rapidly over time as perennial species replace less desirable annual and forb species (Foster and Stubbendieck 1980, Kjar and Stubbendieck 1980). Foster and Stubbendieck (1980) found that vegetation was sparse on gopher mounds <1-year-old and that frequency of perennial grasses increased with mound age while frequency of annual grasses and forbs decreased; the highest increases over 4 years occurred for blue grama (from 2 to 18%), needle and thread (0-63%), prairie junegrass (*Koeleria cristata*) (0-19%), and western wheatgrass (0-24%). After heavy livestock grazing, rangeland improvement through natural plant succession was delayed on areas disturbed by plains pocket gophers (Laycock 1958, Foster and Stubbendieck 1980).

In addition to causing a biomass decrease, pocket gopher mounds may contribute to soil erosion (Foster and Stubbendieck 1980). Northern pocket gophers in Colorado were the principal agent causing erosion (Thorn 1977). At a 11 × 5 m plot, 874 kg of soil had been removed by erosion, equivalent to a plotwide surface lowering of 1.2 cm. Erosion rates caused by pocket gophers were higher than those attributed to other processes in the area.

Unequal displacement of soil by gophers may result in formation of mima mounds (Branson et al. 1965, Murray 1967, Turner et al. 1973, Cox 1990). Such mounds are usually 0.3 to 0.9 m high and 4.5 to 30 m in diameter and are formed over decades as gopher burrowing activities tend to move soil toward the nest (Arkley and Brown 1954, Cox 1984, Cox and Allen 1987). The soil on mima mounds may differ considerably from adjacent soils, having a lower bulk density, higher water permeability, higher organic matter content, and a lack of definite structure in the topsoil (Ross et al. 1968). Stones of the sizes pocket gophers can move are concentrated in mounds (Cox 1984, Cox and Allen 1987) and vegetation on mounds is usually denser and more effective in retarding soil erosion than that off mounds. In a Colorado range seeding project, grasses produced 2 to 5 times more herbage on mounds than between mounds (McGinnies 1960).

Nutrient cycling may be affected by deposition of soil by pocket gophers. Laycock and Richardson (1975) determined that organic matter, nitrogen, and phosphorus increased in areas occupied by pocket gophers. In contrast, other researchers reported reduced nutrients in occupied areas. Grant and McBayer (1981) measured nutrient content of soil samples from old mounds, new mounds, and away from mounds (controls) and found that old mounds were often significantly lower in nutrient concentrations than new mounds, which were lower than controls. McDonough (1974), Reichman and Smith (1985), and Inouye et al. (1987) reported that gophers reduced the average nitrogen concentration near the soil surface and increased the variability in soil nitrogen. Spencer et al. (1985) found soil deposited by pocket gophers to be lower in nutrient content (i.e., phosphorus, nitrate, and potassium) than randomly collected samples; they theorized that the subsoil deposited on the surface by pocket gophers has had nutrients both leached from it and drawn from it by plant roots. The deficiency of nutrients in mounds may also occur because mounds lack the litter layer that is important in holding moisture and nutrients near the surface. The reduction in average soil nitrogen affects plant species composition and slows succession (Inouye et al. 1987); by creating openings in vegetation that are low in nitrogen and high in light, gopher mounds create conditions typical of the early stages of succession.

Some activities of pocket gophers may be beneficial to rangeland. Gophers loosen compacted soil, allowing better aeration and increased water infiltration, and increase soil fertility by adding excrement and burying vegetation. Soil in newly formed mounds often is more friable than adjacent soil (Turner et al. 1973), so this loose soil may increase the infiltration of water (Hansen and Morris 1968) and retard runoff (Abaturon 1968).

Grant et al. (1980) and Spencer et al. (1985) found that the decrease in biomass caused by mounds is partly compensated for by increased production in areas immediately adjacent to mounds, where production was roughly 5.5% higher than vegetative production 40 or 50 cm from the edge of mounds (Grant et al. 1980, Williams et al. 1986). The researchers hypothesized that increased density of vegetation near mounds is a response to increased nutrient availability caused by leaching of nutrients from mounds into surface soil.

Associations With Other Animals

A variety of animals occupy abandoned pocket gopher burrows, including deer mice (*Peromyscus* spp.), pocket mice (*Perognathus* spp.), kangaroo rats, voles, ground squirrels, and weasels. In addition, numerous reptiles and amphibians have been observed or captured in active and abandoned gopher runways (Howard and Childs 1959, Vaughan 1961, Hansen and Ward 1966). Major predators of pocket gophers include weasels, which pursue the gopher in its tunnel system, and badgers, which are adept at digging them out. Coyotes are common predators but pocket gophers probably make up only a small percentage of the coyote's diet (Sperry 1941). Other predators prey on gophers when they are above ground feeding or constructing their mounds, including bobcats, foxes (*Vulpes* spp. and *Urocyon cinereoargenteus*), skunks (*Mephitis* spp. and *Spilogale* spp.), great horned owls, great gray owls (*Strix nebulosa*), barn owls (*Tyto alba*), long-eared owls (*Asio otus*), burrowing owls, red-tailed hawks, Swainson's hawks, goshawks (*Accipiter gentilis*), sparrow hawks (*Falco sparverius*), and snakes (Tryon 1943, Fitch et al. 1946, Evans and Emlen 1947, Fitch 1947b, Tryon 1947, Moore and Reid 1951, Craighead and Craighead 1956, Howard and Childs 1959, Hansen and Ward 1966). Dispersing pocket gophers probably are the most vulnerable to predation, as they have no established burrow systems and sometimes travel above ground (Howard and Childs 1959).

Effects of pocket gopher activities on populations of small mammals have not been well studied. However, some general effects can be inferred. Litter can be substantially reduced by pocket gopher activity. Because reduction in litter tends to make the habitat more suitable for deer mice and less suitable for voles, populations of deer mice would tend to increase and voles to decrease. Furthermore, gophers compete directly with voles for food (Ward 1960, Johnson 1964).

Management

Proper range management can favor populations of plains pocket gophers, which are attracted to areas of high and improving range condition, where they use vigorous plants. Once present, pocket gophers interact with grasslands and livestock in ways that can decrease rangeland productivity by 25 to 50%. Range managers therefore need to be aware that the presence of pocket gophers may necessitate some reduction in livestock grazing to maintain good range condition.

Despite lowered rangeland production where pockets gophers occur, many researchers believe that gophers are not a significant problem on well-managed rangelands (Turner et al. 1973),

and in some areas, such as high mountain rangeland, the total ecological effects of pocket gopher populations may be beneficial rather than detrimental. Where livestock were excluded, Turner (1969) found the largest grass biomass increase on range with pocket gophers, so it is possible that pocket gophers may actually improve depleted range. Presently, pocket gopher control is rarely practiced on western rangelands and control is more frequently recommended for improving deteriorated rangelands than for maintaining rangelands that are well managed and productive. Where range condition is poor, it may occasionally be advantageous to reduce pocket gopher populations; for example, production on deteriorated mountain rangeland in Colorado increased 290 kg/ha (mainly perennial dicots) after pocket gopher control (Turner 1969). However, even on ranges where gophers are numerous, overgrazing by livestock is frequently the primary cause for deterioration of vegetation cover (Ellison 1946).

Because trapping is extremely slow, time consuming, and practical only in small areas, the most widely used approach to alleviate pocket gopher damage is poisoning. Poisons are distributed either by hand baiting in each burrow system or by a burrow-builder, which creates an artificial burrow and places bait in that burrow (Case 1983). Indirect or ecological control involves habitat modification to make the area less suitable for pocket gopher occupation. Control of forbs, which frequently have large underground storage structures, can be an effective method for minimizing damage to rangeland by northern pocket gophers. Application of 2,4-D herbicide in Colorado reduced pocket gopher populations by 80 to 90%. Success was attributed to decreased forb production (Keith et al. 1959, Hansen and Ward 1966, Tietjen et al. 1967) and resulting starvation of pocket gophers. Where vegetative composition after herbicide treatment remained relatively stable for 5 years (with a grass dominance), repopulation of treated areas was slow. Howard and Childs (1959) also found that herbicide spraying or burning depleted the forb supply and greatly reduced valley pocket gopher numbers. Reduction of forbs is less effective for reducing plains pocket gopher populations, as they survive well on warm-season prairie grasses that have large root to stem ratios.

Other management techniques are needed, particularly for plains pocket gophers. Also, a long-term comprehensive cost-benefit analysis of pocket gopher control needs to be completed that would include reinvasion rates by pocket gophers. Where pocket gophers have been removed from rangeland, it would be advantageous to have a repellent available for use in burrow systems to prevent rapid reinvasion of those burrows by other gophers. In addition, more data are needed on how to manage for good range productivity, in the presence of pocket gophers and after control. For example, what effects do fertilization, reseeding, and manipulation of grazing patterns (such as rest or light grazing) have on rangelands before and after pocket gopher control?

The importance of pocket gophers as a component of grassland ecosystems becomes evident as we consider their role as prey items and their influence on soils, microtopography, habitat heterogeneity, plant species diversity, and primary produc-

tivity. Management efforts for rangeland must be based on a balanced ecological approach that takes all of these influences into consideration.

OTHER SMALL RODENTS

General Effects of Grazing on Small Rodents

Variable effects of grazing on small mammals depend on the level of grazing, the type of grassland, and the particular small mammal species involved. Moderate grazing may have little effect or even a positive effect on many species, but overgrazing depresses populations of most small mammals. For example, heavy grazing and repeated fires in sagebrush range caused the establishment of nearly pure stands of annual grasses (cheatgrass [*Bromus tectorum*] and medusa-head [*Taeniatherum asperum*]) over vast areas of southern Idaho (Stewart and Hull 1949, Hironaka 1961). Such sites support only a few deer mice and Great Basin pocket mice (*Perognathus parvus*). In southern Idaho, rodent burrow numbers were significantly higher on ungrazed than on heavily grazed pastures (Anderson 1972), and in a seldom grazed pasture in Arizona, the total rodent population was roughly twice as high as on a heavily grazed pasture (Gallizioli 1979). Carothers et al. (1976), in a study of the impact of burros (*Equus asinus*) on a desert region at the Grand Canyon, found higher total numbers and a greater diversity of small mammals on an area devoid of burros compared to an adjacent heavily grazed area. When range abuse is continued for decades as it has been in certain areas of the West and Southwest, the inevitable severe soil erosion reduces the quality of the habitat for even grazing-tolerant species like kangaroo-rats, prairie dogs, and jackrabbits.

Consistent heavy grazing can reduce the number of species present in an area, but moderate or light grazing may have no effect or can sometimes even promote species diversity. Oldemeyer and Allen-Johnson (1988) studied effects of grazing on small mammal populations on the Sherburne National Refuge, Idaho, where sagebrush and mountain mahogany (*Cercocarpus montanus*)-dominated ecosites were grazed under a deferred-rotation grazing system (grazed mid-Jun to early Aug in 1 year and early Aug through late Oct the next year). They concluded that the grazing regime had no discernible impact on the relative abundance and diversity of small mammals, or on populations of the 2 most abundant species (deer mice and least chipmunks [*Eutamias minimus*]), 4 and 5 years after its implementation. Moulton (1978) and Moulton et al. (1980) found that moderate grazing of cottonwood (*Populus* spp.) riparian woodland provided habitat opportunities for twice the number of species as an ungrazed area. In this case the grazed area had been managed for 17 years at a moderate stocking rate under a spring deferment and a July to December grazing season. This grazing management system promoted microhabitat and edge diversity by allowing patchy habitats to develop and provided niches for a greater variety of small mammals. In contrast, secondary succession on the ungrazed site led toward more uniform plant composition and fewer small mammal species.

Several theories have been tested to explain the presence of small mammals on grasslands, including the size and availability of food and the structural attributes of the habitat. Animal species diversity has often been dependent on habitat structural diversity (Pimlott 1969, Pianka 1973); research by Grant et al. (1982) suggests that this concept is true for grasslands, where the general composition of small mammal communities is determined primarily by habitat structural attributes. Livestock grazing, through selective defoliation of forage species, affects many aspects of grassland ecosystems, including plant cover or biomass, plant species composition and diversity, primary productivity, soil compaction, and soil moisture. These changes can drastically alter the structural attributes of the ecosystem. Plant cover probably has the most influence on small mammal population abundance because it provides food, nests, and protection from predators. Amount of plant cover also influences behavioral interactions such as fighting and dispersal (Warnock 1965, Krebs 1970, Krebs et al. 1973, Myers and Krebs 1974), and moderates ground level humidity, temperature, and soil moisture (Birney et al. 1976). Mulch, a by-product of cover, modifies surface temperatures and retards evaporation (Hopkins 1954). Removal or alteration of cover can cause changes in small mammal communities (LoBue and Darnell 1959, Birney et al. 1976, Geier and Best 1980, Grant et al. 1982). MacCracken et al. (1985a) found a significant positive relationship between small mammal abundance and canopy cover in sagebrush-grass rangeland in Montana, where all areas were managed on a rest-rotation grazing system. Geier and Best (1980) found that, of plant life forms, percentage forb cover was most consistently correlated with small-mammal species abundances, grass coverage was of lesser importance, and tree cover was not related to species abundance. They found a significant correlation between the abundance of woody plant debris (e.g., logs, brushpiles, stumps) and small-mammal numbers. These data are consistent with that of Steenbergh and Warren (1977), who reported that rodent abundance and diversity increased with vegetation cover and density and that overgrazing by cattle decreased vegetation complexity. Hanley and Page (1982) observed that grazing altered rodent species diversity through changes in plant species diversity on several habitats in northeastern California.

In assessing grazing impacts on small mammal communities, Hanley and Page (1982) stressed the importance of evaluating effects on a habitat-type basis. Grant et al. (1982) also concluded that the response of small mammals to grazing depends on the site and the original mammal species composition and therefore differs greatly between grassland types; they found differential changes in several small mammal community parameters between grazed and ungrazed sites in 4 Western grassland communities. Where there is sufficient vegetation in ungrazed grasslands to support herbivorous, litter-dwelling species, the small mammal communities are changed significantly by a reduction in vegetation cover caused by grazing. This is true for tallgrass and montane grasslands, which have significantly greater standing vegetation, greater annual net primary production, and greater abundance of such mammals than shortgrass and bunch-

grass grasslands (French et al. 1976, Grant and Birney 1979, Grant et al. 1982). The reduction in vegetation cover on tallgrass grazed sites may bring cover below the level required to support dense populations of herbivorous, litter-dwelling small mammals such as voles (Birney et al. 1976, Grant et al. 1982). The result is a decrease in total small mammal biomass, an increase in small mammal species diversity, and a shift from litter-dwelling species with relatively high reproductive rates to surface-dwelling species with relatively low reproductive rates. In studies by Grant et al. (1982), microtines dominated ungrazed tallgrass grassland, with cricetines roughly half as abundant. In contrast, grazed tallgrass grassland was dominated by sciurids and heteromyids. In montane grasslands, grazing-induced reduction in cover resulted in similar decreases in total small mammal biomass and changes in species composition from litter-dwelling species to surface dwelling species, but resulted in a decrease rather than an increase in species diversity. At montane sites microtines dominated the ungrazed area but cricetines dominated the grazed area (Grant et al. 1982). In shortgrass and bunchgrass grasslands (where plant cover was already low) small mammal faunas and abundance were not changed drastically by further reduction in vegetation cover by grazing (Moulton 1978, Grant et al. 1982). Small mammal communities of shortgrass and bunchgrass are frequently composed primarily of surface-dwelling, granivorous and omnivorous species adapted to an open habitat. Grant et al. (1982) found that on bunchgrass grassland sciurids and heteromyids were dominant, and on shortgrass grassland biomass was greatest for cricetines and sciurids, followed by heteromyids. A reduction in cover may actually improve conditions for granivorous rodent species (Baker 1971, Grant et al. 1982), because grazing can increase the abundance of annual grasses and forbs, which produce more seeds than the perennial grasses that are reduced in abundance by grazing. Plant species composition does not appear to be as important a structural attribute as cover in determining rodent species composition. For example, treatment of shortgrass prairie with fertilizer caused a marked increase in vegetation cover and a subsequent immigration of prairie voles (*Microtus ochrogaster*), but did not significantly change plant species composition (Grant et al. 1977). These studies suggest that the effect of grazing on small mammals will be related to the extent to which a habitat can be perturbed. Tallgrass habitats (such as at riparian sites) potentially can be transformed by grazing to midgrass, mixed grass, or shortgrass habitats. Midgrass habitats (i.e., sand sagebrush) can be transformed to shortgrass, but shortgrass remains shortgrass.

Small mammals in riparian habitats can be significantly impacted by grazing. Kauffman et al. (1982) compared small mammal populations before and after late season (late Aug to mid-Sep) grazing. Population estimates decreased in all habitats, from 800 to 83 mammals/ha in hawthorne (*Crataegus* spp.) communities, from 450 to 60 mammals/ha in meadow communities, and from 129 to 42 mammals/ha in cottonwood-mixed conifer communities. Population estimates in ungrazed areas changed during this same time period from 690 to 136/ha in hawthorne communities, from 235 to 463/ha in meadow communities, and from 118 to 254/ha in cottonwood communities.

The significant decrease in small mammal populations in grazed areas was apparently caused by a loss of cover due to forage removal, resulting in increased predation and immigration out of grazed habitats into neighboring ungrazed habitats.

In the Great Basin region of the United States, the quality of habitat for small mammals is also strongly dependent upon habitat structural features (Hanley and Page 1982). Overgrazing by domestic cattle and sheep during the late 1800s drastically altered plant communities in the Southwest (Griffiths 1902, Barnes 1936), resulting in severe depletion of vegetation cover by 1900. Much of the Great Basin once dominated by perennial grasses is currently dominated by desert shrubs (Hastings and Turner 1965, Hanley and Page 1982), including creosote (*Larrea tridentata*), tarbush (*Flourensia cernua*), mesquite (*Prosopis juliflora*), Mormon tea (*Ephedra trifurca*), and acacia (*Acacia* spp.). The effects of livestock grazing on plant life form diversity, and subsequently on rodent species diversity, differ greatly by habitat. Despite long-term protection from grazing, vegetation patterns on desert grasslands have not readily reverted to their original grass cover (Chew 1982, Roundy and Jordan 1988, Heske and Campbell 1991), perhaps because recovery takes a very long time in desert environments or because, once established, woody plants may competitively restrict the reestablishment of herbaceous cover and perennial grasses (Anderson and Holte 1981, West et al. 1984, Daddy et al. 1988). These vegetation changes have caused changes in rodent populations. For example, reduction of herbaceous vegetation and increased abundance of shrubs as a result of livestock grazing have resulted in an increase in plant life form diversity in the most mesic habitats; this is associated with increased rodent diversity (i.e., rodent species richness and evenness), probably because of increased diversity of seed size, seed type, and microhabitat. Generalist granivorous foragers like the least chipmunk, Great Basin pocket mouse, and deer mouse have increased most in mesic habitats. In contrast, reduction of herbaceous vegetation by livestock grazing has resulted in a reduction in plant life form diversity and rodent diversity in xeric communities.

Small Rodent Species Adversely Affected by Grazing

Some rodents may be adversely affected by livestock grazing through depletion of food resources, including wood rats (*Neotoma* spp.) (Steenburgh and Warren 1977), antelope squirrels (*Ammospermophilus* spp.) (Steenburgh and Warren 1977), cotton rats (*Sigmodon hispidus*) (Goertz 1964, Feldhamer 1979), Townsend moles (*Scapanus townsendi*) (Kuhn et al. 1966), voles (Birney et al. 1976), harvest mice (*Reithrodontomys* spp.) (Black and Frischknecht 1971), jumping mice (*Zapus princeps*) (McGee 1982), and masked shrew (*Sorex cinereus*) (McGee 1982). Steenburgh and Warren (1977) found woodrats (*Neotoma albigula*) more common in areas with greater vegetation cover, and away from intensively grazed areas. Vorhies and Taylor (1940) noted that on ranges not overgrazed by domestic stock, the wood rat, by feeding preferentially on woody plants and weedy herbs, can aid in reestablishment of climax perennial grasses. Antelope squirrels eat mostly green

grasses, which are also eaten by livestock (Howard et al. 1959, Bradley 1968, Hawbecker 1975). Wood (1969) found that antelope squirrels were most abundant in creosote and climax grassland areas, 2 vegetation types not likely to be overgrazed.

Cotton rats are restricted to the abundant cover of undisturbed grassland (Phillips 1936, Smith 1940, Whitford 1976, Feldhamer 1979). Their populations correlated positively with density and height of perennial grass cover (Goertz 1964) and they do not use heavily grazed areas. Fleharty and Mares (1973) reported that cotton rats preferred habitat with dense undergrowth and protective overstory and Guthery et al. (1979) reported densities 4 times greater on areas with a greater vegetation biomass. Cotton rat populations were low where cattle grazing reduced grass cover; yet where cattle were excluded and there was nearly complete grass cover, populations of cotton rats increased (Whitford 1976).

Cattle grazing impacts from trampling were a significant factor on nestling mortality of Townsend moles in wetland pastures of western Oregon (Kuhn et al. 1966). Normal grazing activities on soft ground early in the season permitted the cattle's hooves to break through the sod and crush the nestlings.

Voles. Most vole species (Fig. 16) select good cover, so increased canopy cover is important in increasing Microtine populations (Zimmerman 1965, Getz 1971, Hodgson 1972, Douglas 1973, Birney et al. 1976, Feldhamer 1979, Grant et al. 1982). Prairie voles generally inhabit areas with dense stands of lush vegetation (Jameson 1947, Carroll and Getz 1976, Abramsky 1978, Abramsky et al. 1979, Fleharty and Navo 1983). They do well in ungrazed or only lightly grazed grasslands but disappear from areas with moderate to heavy grazing (Birney et al. 1976, Moulton 1978). In a study by Agnew et al. (1986), prairie voles were only captured on mixedgrass prairie sites and did not occur on shortgrass sites such as prairie dog colonies. Kauffman et al. (1982) found that the mountain vole (*Microtus montanus*) was also drastically reduced in numbers or disappeared from habitats due to grazing. Studies of vole cycles by Birney et al. (1976) emphasize the importance of cover because at widely distant sites

in the western United States, populations of prairie voles and meadow voles (*M. pennsylvanicus*) cycle where the grasslands are dense but not where grasses are kept low by burning or grazing. Birney et al. (1976) showed a significant increase in vole populations after cessation of grazing in a tallgrass prairie, from only 1 individual/ha on a grazed area versus 24/ha on an ungrazed area. Vole populations on a grazed mid-grass prairie in South Dakota were only 2.8/ha, similar to shortgrass prairie populations in Colorado, where prairie voles on an ungrazed area reached a high of only 3.5 individuals/ha, and these individuals may have been transients. Cover, especially litter, was low on both the grazed South Dakota and ungrazed Colorado grasslands and was apparently not sufficient for vole populations to exceed the increase phase of a population cycle. Birney et al. (1976) hypothesized that there may be a cover threshold (between 400 g/m² and 600 g/m²) required before cycles can occur, and that a lower threshold may have to exist before voles can establish resident breeding populations. These researchers postulated that cover provides favorable conditions for population build-ups by providing food, reducing antagonistic contacts between voles, and moderating microhabitat humidity and temperature.

During normal years, voles have little influence on grasslands, although they may have a direct impact on soil. Golley et al. (1975) pointed out that voles at a density of 200-400/ha probably dislodge 1,000 m³ of earth/ha/year. Because this activity is restricted to the top 40 cm of soil, such activities influence microtopography and surface water runoff. Voles normally have little effect on vegetation cover because the amount of standing crop vegetation they remove is usually quite small, ranging from 1-35% (Krebs and Myers 1974, Batzli 1975), with the higher figure being unusual. However, Batzli and Pitelka (1970, 1971), after study of the California vole (*Microtus californicus*) in the field, and Krebs and Myers (1974), after review of literature, concluded that during the late increase and peak phases of a population cycle, grazing by voles can have a marked effect on vegetation cover. Foster (1965) found that grazing by microtine rodents removed current-season stem primordia of perennial grasses. And in a series of exclosure experiments, Batzli and Pitelka (1970) showed that grazing by voles kept the habitat open and increased plant species diversity; if voles were excluded, grasses, the preferred food type, increased and became dominant. In some instances, voles can have severe effects on vegetation. Batzli and Pitelka (1970) found that a population of California voles that exceeded 1,500 voles/ha removed 85% of the volume of vegetation for wild oats (*Avena fatua*), Italian ryegrass (*Lolium multiflorum*), and ripgut grass (*Bromus rigidus*). Heavy cropping of plants during reproduction suppressed flowering and caused a 70% seed loss (Batzli and Pitelka 1970). Seed predation by mice, including voles, may be an important regulating factor for some plant species (Janzen 1971). In California annual grasslands, mice at densities of 296/ha consumed 65 to 75% of wild oat seed (Marshall and Jain 1970, Borchert and Jain 1978); these seeds were chosen twice as frequently as those of other plant species, even though they were only 4% of the total plant cover.

During cyclic population peaks, voles (*M. longicaudus*, *M. montanus*, and *M. pennsylvanicus*) can reach densities

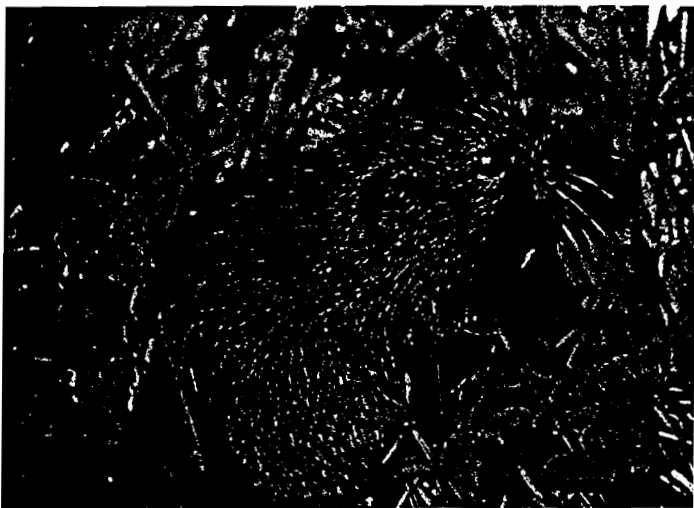


FIGURE 16. Most vole species, such as *Microtus canicaudus*, inhabit areas with dense vegetative cover, and populations decline under heavy grazing. Photo by J. Wolfe.

$\leq 7,400/\text{ha}$ (Spencer 1958). At these high population levels, voles can kill and damage sagebrush and other shrub species (Mueggler 1967, Phillips 1970, Frischknecht and Baker 1972) by stripping bark from plants and girdling stems and branches. Damage is greatest when a dense, ungrazed herbaceous understory exists that favors vole population increases, and when the snowpack persists throughout the winter (Mueggler 1967, Frischknecht and Baker 1972). Usually voles kill only portions of the crowns of individual plants but occasionally entire plants are killed. During 1962-1964, Mueggler (1967) observed an irruption of voles on southwestern Montana rangeland that caused damage to a number of shrubs, including big and silver sagebrush (*Artemisia* spp.), sumac (*Rhus trilobata*), bitterbrush (*Purshia tridentata*), mountain mahogany, and serviceberry (*Amelanchier alnifolia*). Mueggler (1967) recorded crown kills of 35 to 97% of sagebrush on extensive areas, with $> 80\%$ of the stand killed in some areas. A similar population explosion of long-tailed voles (*M. longicaudus*) in Utah in 1969 killed 59% of sagebrush plants and damaged another 28% (Frischnecht and Baker 1972). If peaks in population could be predicted, voles could be used to control undesirable shrubs. However, as natives of the sagebrush-grass ecosystem, normal vole populations have little impact on rangeland. Factors responsible for population irruptions and methods of inducing them would have to be identified before voles could be effectively used for biological control of sagebrush.

Sagebrush voles (*Lagurus curtatus*) occur in the most xeric habitats occupied by microtines (O'Farrell 1972) and are 1 of the rarer species of voles. Rickard (1960) and O'Farrell (1972) suggested that the distribution of the sagebrush vole was restricted to areas where big sagebrush (*Artemisia tridentata*) occurs along with associated large bunchgrasses such as bluebunch wheatgrass (*Agropyron spicatum*). Hall (1946) stated that big sagebrush was one of the main foods of sage voles. However, Moore (1943) found little evidence of feeding on sagebrush; and Hansen (1956), Maser (1974), Maser and Strickler (1978), and MacCracken et al. (1985a), found that good grass cover, not sagebrush, was the limiting factor for sage vole distribution. Maser (1974) and Maser and Strickler (1978) found voles only in the best rangeland and not on overgrazed, predominantly sagebrush-covered habitat. Oldemeyer et al. (1983) and Oldemeyer and Allen-Johnson (1988) found sage voles more abundant on ungrazed rangeland (with greater plant biomass) than on grazed rangeland in Nevada. Sagebrush voles were found to be beneficial to fescue-dominated (*Festuca* spp.) rangeland in Oregon (Maser and Strickler 1978) because voles deposit vegetation and fecal pellets around the grass that make nutrients available to the fescue plants. Sagebrush voles are not a concern from an economic standpoint; their feeding habits cause little observable permanent damage to rangeland and may help foster grass seed germination (Maser 1974).

Harvest Mice. Western harvest mice (*Reithrodontomys megalotis*) and plains harvest mice (*R. montanus*) usually occur in tall, dense grass habitats (Quast 1950, Maxell and Brown 1968, Armstrong 1972, Larrison and Johnson 1973, Whitford 1976, Ford 1977, Feldhamer 1979). The optimum habitat for western har-

vest mice is lush vegetation, usually grassy, weedy habitat with 90-99% cover (Whitford 1976, Ford 1977, Abramsky 1978, Abramsky et al. 1979, Fleharty and Navo 1983). Western harvest mice are therefore most abundant on rangeland with no or relatively light grazing (Black and Frischknecht 1971). Moderate grazing tends to diminish their numbers until populations disappear when heavy grazing leads to range depletion and reduced grass cover (Whitford 1976). Western harvest mice were found by Agnew et al. (1986) to occupy mixed-grass prairie sites only; they do not occupy short grass sites such as prairie dog colonies. Plains harvest mice were found by Kaufman et al. (1990) to be the most restricted in distribution of the species studied; they would be severely impacted if their preferred habitat (upland mixed-grass prairie) were altered by grazing.

Species Not Affected or Affected Favorably by Grazing

Populations of a few species of small rodents may be increased where livestock are grazed, including the least chipmunk, deer mice, some pocket mice, and numerous kangaroo rats.

Chipmunk. The least chipmunk is an opportunistic forager and is the most widespread of all North American chipmunks (Hall 1981), suggesting that they adapt rapidly to a variety of habitats (Sullivan 1985). Range depletion favors an increase in least chipmunk density; they were found most common in depleted shadscale (*Atriplex* spp.), where numbers were 10 times greater than in stands in better condition (Larrison and Johnson 1973), and in grazed sagebrush-fescue sites, where they were 4 times more abundant than in ungrazed sites (Hanley and Page 1982). Chipmunks and golden mantled ground squirrels (*Spermophilus lateralis*) have been found to favor the spread and increase of bitterbrush by storing seed in surface caches (Hornmay 1943).

Deer Mice. Deer mice (Fig. 17) and white-footed mice (*P. leucopus*) are pioneer species that occur in most vegetation types during most stages of plant succession, but usually not in large numbers (Geier and Best 1980). The deer mouse is a widespread and adaptable species with broad diets, occupying sites ranging

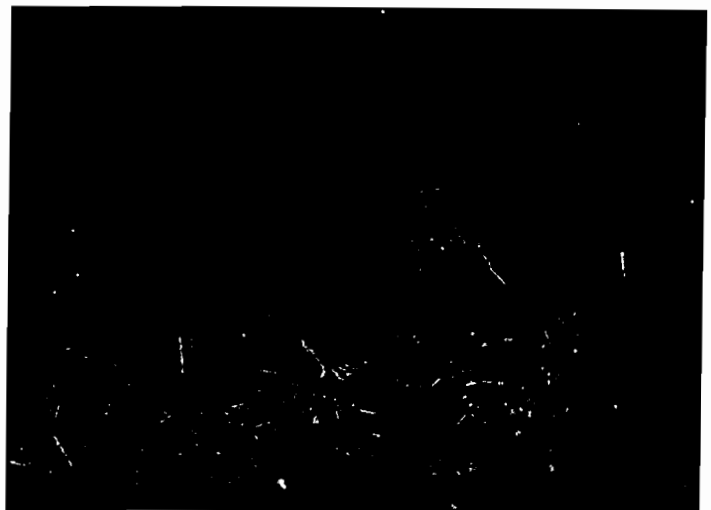


FIGURE 17. Grazing is often beneficial to the white-footed deer mouse (*Peromyscus maniculatus*), a widespread and adaptable species. Photo by E. Kalmbach.

from native prairie to croplands (Kaufman et al. 1990, Feldhamer 1979). It is sometimes referred to as a weed species, because disturbances that result in early seral stages favor population increases (Williams 1955, Armstrong 1977), and it is usually the most abundant small mammal in severely disturbed areas (Halvorson 1982). Therefore, grazing is generally beneficial to deer mice (Phillips 1936, Harris 1971, Moulton 1978), which select areas with low cover (Black and Frischknecht 1971) and are common in habitats with bare soil surface and open vegetation such as grazed prairie (Phillips 1936, Quast 1950, Grant et al. 1982). Researchers have found that heavy grazing in big sagebrush habitat promotes an increase in deer mice numbers (Black and Frischknecht 1971, Larrison and Johnson 1973). Kaufman et al. (1982) found that the total small mammal population declined in grazed communities, but the density estimates of deer mice increased; they were dominant after the grazing season while they were found in only minor proportions before. Feldhamer (1979) and Oldemeyer and Allen-Johnson (1988) noted that deer mice used microhabitats with greater shrub intercept, which would be the case in grazed areas.

However, range depletion in all habitats does not always favor an increase in deer mouse populations. Hallett (1982) did not find deer mice associated with any measured habitat variable. Geier and Best (1980) found increased deer mice populations with increasing forb cover, and Fitzgerald (1978) found more deer mice in an ungrazed than in a grazed riparian habitat, but fewer deer mice in an ungrazed than in a grazed short-grass prairie upland. Hanley and Page (1982) concluded that deer mice have differential responses to grazing, decreasing in the most xeric habitats and increasing in mesic habitats.

Deer mice do not normally have an effect on rangeland vegetation. However, seed predation by mice may be an important factor in northwest rangelands. During reseeding efforts, deer mice may consume or cache considerable seed, resulting in poor plant establishment. In contrast, West (1968) concluded that seed caches may result in clumps of seedlings and that 50% of bitterbrush and 15% of ponderosa pines (*Pinus ponderosa*) in Oregon resulted from rodent seed caches.

Effects of Grazing on Desert Rodents

Desert shrub-grasslands in the Southwestern United States are ephemeral environments characterized by seasonal bursts of vegetation productivity after sporadic rains (Reichman 1975). Vegetation is composed of desert shrubs, drought resistant summer-growing perennial grasses, and annual plants. Much of this area is rangeland used primarily for grazing livestock. Seeds persist after green vegetation is gone and are therefore the dominant items in rodent diets. The most specialized granivorous rodents in North American deserts belong to the family Heteromyidae, which includes the pocket mice, kangaroo rats, and kangaroo mice (*Microdipodops* spp.). These rodents feed almost exclusively on seeds and are efficient at locating and harvesting them. The rodents are nocturnal, have external cheek pouches (permitting collection and movement of large quantities of seeds during each foraging bout), and highly efficient kidneys, which enable them to excrete nitrogenous wastes and

maintain osmotic balance on a diet containing little free water (Eisenberg 1963, Schmidt-Nielsen 1964). Pocket mice use areas beneath and around shrub canopies (Brown et al. 1979b) where average seed densities are higher and more uniform than in open microhabitats. Bipedal kangaroo rats and kangaroo mice forage primarily in open spaces between perennial vegetation (Brown et al. 1979b), where they move rapidly and efficiently between widely spaced seed clumps. Grasshopper mice (*Onychomys* spp.) are commonly found in areas with open vegetation (Abramsky et al. 1979) but are not closely associated with particular habitats in the desert Southwest rangeland, probably because of their insectivorous diet (Hallett 1982).

Pocket Mice. Pocket mice respond differently to heavy grazing depending on the species involved. Most pocket mice species prefer a heavy protective cover of grass and some shrubs (Reynolds and Haskell 1949). In desert Southwest rangeland, pocket mice forage under and around large bushes and clumped vegetation (Rosenzweig 1973, Wondollock 1978) and are common only if bushes form an important proportion of the vegetation (Rosenzweig and Winakur 1969). Feldhamer (1979) found Great Basin pocket mice resident only in relatively dense cover in sagebrush or greasewood communities. Within this habitat, densities were highest when sand was present, probably because of the limited ability of pocket mice to dig through hard clay soils. These pocket mice are most common in non-grazed dense grass communities or areas of relatively light grazing with heavy cover and seed production, and numbers are reduced in habitats sustaining heavy grazing (Black and Frischknecht 1971, Larrison and Johnson 1973, Hanley and Page 1982). Price (*P. penicillatus*) and Bailey (*P. baileyi*) pocket mice (Reynolds and Haskell 1949) are also most abundant in dense stands of perennial grasses and their numbers are reduced on grazed ranges (Steenbergh and Warren 1977).

The Arizona pocket mouse (*Perognathus amplus*) has been associated with open habitat and increased grazing (Bond 1945, Rosenzweig and Winakur 1969). Guthery et al. (1979) found the greatest densities of silky pocket mice (*Perognathus flavus*) where there was the sparsest grass cover and found them adversely affected by protection of the playa grassland from grazing. Also, hispid pocket mice (*Perognathus hispidus*) are commonly found in areas with open vegetation (Abramsky et al. 1979) or where the prairie is intensely grazed and erosion has removed much of the topsoil (Smith 1940). Hispid pocket mice inhabit a wide variety of habitats, from native prairie to croplands, and would therefore be expected to be little affected by disturbance (Kaufman et al. 1990, Feldhamer 1979). However, severe disturbance limits their populations, and Agnew et al. (1986) found hispid pocket mice occupying mixed-grass prairie sites but not heavily grazed prairie dog colonies.

Pocket mice are unimportant with regard to their effects on rangeland grasses. Grazing itself, by reducing the height of bunchgrasses, produces a less favorable habitat, and lowers pocket mouse numbers.

Kangaroo Rats. Throughout the southwestern United States, kangaroo rats occur in great numbers in desert shrub-grasslands. Most species of kangaroo rats avoid dense herbaceous vegeta-

tion, including the narrow-faced kangaroo rat (*Dipodomys venustus*) (Hawbecker 1940), the Tulare kangaroo rat (*D. heermanni tularensis*) (Fitch 1948), and Heerman's kangaroo rat (*D. h. sayatilis*) (Dale 1939). Ord's kangaroo rat (*D. ordii*), has a wide distribution that includes relatively nonproductive habitats (Rosenzweig and Winakur 1969, Brown 1975, Frye 1983) and is most abundant where disturbed earth provides easy tunneling, such as along roadsides (Larrison and Johnson 1973). The Texas kangaroo rat (*Dipodomys elator*) is restricted to mesquite grassland of northcentral Texas, where it is a threatened species (Stangl et al. 1992). This species shows a preference for heavily grazed short-grass areas with exposed earth resulting from concentrated traffic of vehicles and livestock. Habitat modification by grazing has been proposed to ensure the viability of local populations or to permit the existence of the species elsewhere. Such changes, in fact, may duplicate past habitat modification effects of bison and prairie dogs, and regularly occurring fires on mesquite grasslands.

Populations of Merriam kangaroo rats (*D. merriami*) (Fig. 18) are also favored by grazing. The range of this species, which is widespread in the Southwest, coincides with the distribution of creosotebush, low humidity and rainfall (<24.5 cm annually), high summer temperatures and evaporation rates, and a lightly textured soil favorable to burrowing (sandy or sandy loam) (Reynolds 1958). Most of the lands inhabited by Merriam kangaroo rats are managed primarily as rangelands for cattle grazing (Reynolds 1958). On higher elevation rangelands, maintenance of a perennial grass cover with interspersed shrubs furnishes livestock grazing and reduces erosion; at lower, drier elevations a shrubby cover is all that can be maintained. When rangelands are improperly grazed, there is a gradual downward trend in perennial grass density and a corresponding increase in Merriam kangaroo rats, which avoid sites with dense cover (Stamp and Ohmart 1978, Hallett 1982) and prefer open areas with scattered woody plants and annual grasses. Numbers of Merriam kangaroo rats increase with grazing-induced decreasing grass cover and mesquite invasion (Bond 1945; Reynolds

and Glendening 1949; Reynolds 1950, 1958; Rosenzweig and Winakur 1969). When grazing is moderate and percent cover is not decreased, populations of Merriam kangaroo rats have been significantly greater in ungrazed areas (Heske and Campbell 1991); the researchers postulated that cattle had an effect on seed production or plant species composition that was not measured.

There are interspecific differences in the responses of kangaroo rat populations to range depletion. While the species discussed previously are more abundant on grazed sites (Quast 1950, Reynolds 1958, McCulloch 1962), the chisel-toothed kangaroo rat (*D. microps*) is 2 to 3 times more abundant in healthy shadscale than in stands depleted by grazing (Larrison and Johnson 1973). Shadscale leaves comprise most of its diet (Johnson 1961). The banner-tailed kangaroo rat (*D. spectabilis*) is also restricted to highly productive regions of deserts and arid grasslands.

Effects of Seed Foraging by Desert Rodents on Rangeland

Desert rodents are the primary consumers of seeds of annual and perennial plants and act as predators and dispersers of seeds. In arid rangelands, granivory may have an especially pronounced impact on seed densities and distributions, and thus on the plant community as a whole. Heteromyid rodents, including pocket mice and kangaroo rats, are some of the primary seed eaters (Brown et al. 1979b). Up to 95% of the items in kangaroo rat diets are seeds (Reynolds 1958). Heteromyid rodents tend to prefer high density seed patches in their foraging activities (Reichman 1979, 1983; Price and Waser 1985), collecting seeds when abundant and storing them for use when they are scarce. These rodents generally use large seeds >0.25 mg (Price and Reichman 1987). Merriam kangaroo rats forage mainly in open areas (Wondelleck 1978, Rosenzweig 1973) that may have clumped seeds at densities 10-15 times higher than under shrubs (Reichman and Oberstein 1977). Unlike kangaroo rats, pocket mice do not select large seed clumps over small clumps or scattered seeds (Price 1978, Hutto 1978) and they are more efficient at finding smaller, scattered seeds than are kangaroo rats (Reichman and Oberstein 1977). Kangaroo rats escape predators by jumping, and are therefore better suited to open rather than vegetated areas. Pocket mice, however, are better protected from visually hunting predators by remaining in or near vegetation.

Where kangaroo rats live in loose colonies, the plants in the vicinity of the colony are denuded of seeds. Kangaroo rats may harvest > 75% of an entire seed crop (Chew and Chew 1970, Nelson and Chew 1977, Borchert and Jain 1978, Price and Jenkins 1986) and in some years, Merriam kangaroo rats are sufficiently abundant to eat all large perennial grass seed produced (Reynolds 1958). Examination of kangaroo rat burrows by Vorhies and Taylor (1922) and Taylor (1930) showed an average of 1.7 to 1.8 kg of seed material stored in each burrow. With an estimated population of 49 kangaroo rats (≤ 100)/ha, this would amount to 8.3 kg of seeds/ha.

The abundance of plant species whose seeds are favored foods of these small mammals can be strongly affected by seed predation. Soholt (1973) found that in the Mojave desert, kangaroo rats consumed 95% of the seed of Crane's bill (*Erodium cicu-*



FIGURE 18. Populations of Merriam kangaroo rats (*Dipodomys merriami*) are favored by livestock grazing. Photo by E. Kalmbach.

tarium), causing a reduction in the numbers of this plant. Foraging by rodent granivores substantially reduces the standing crop of large-seeded winter annual plants (Brown et al. 1986). After removal of rodents, densities of these plants increased as much as several thousand times. Batzli and Pitelka (1970) and Borchert and Jain (1978) used exclosures to show that rodents can remove the majority of seeds of preferred plant species and that densities of plants can be reduced > 60% by rodent foraging. Brown et al. (1979a) removed heteromyid rodents and ants from plots and found seed densities highest on the plot from which ants and rodents were excluded, intermediate on the plots where either ants or rodents had been removed, and lowest on the control plot where all granivores were present. Densities of annuals and biomass of seeds were about 1.5 times greater on plots where rodents had been excluded than on plots where they were present (Brown et al. 1979a).

The fate of seeds following harvest by rodents is an important determinant of plant population recruitment. Although rodents consume large amounts of seed, their seed caches are a major source of plant recruitment (West 1968, Evans et al. 1983, McAdoo et al. 1983). Kangaroo rats cache seeds in a centrally located burrow, but also often store seed in small scattered caches just below the soil surface. Unrecovered caches provide for recruitment of new plants throughout rodent home ranges. Seedling establishment of annual plants and small-seeded perennial grasses is influenced by pocket mice (LaTourrette et al. 1971) and seedling establishment of large seeds is influenced by kangaroo rats.

Kangaroo rats can have variable effects on condition of desert or arid rangelands. When a range is in good to excellent condition, Merriam kangaroo rats have little effect on seed dispersal (Reynolds 1958); good quality rangeland is less favorable for kangaroo rats because increased cover is an obstacle to escape from predators and because large-seeded vegetation, the preferred food, is replaced by small-seeded plants as increasing perennial grass density forces out weedy annuals. On rangelands in good to excellent condition, the seed burying habits of heteromyid rodents are probably beneficial to rangeland, as large-seeded perennial grasses and tall shrubby plants have been shown to increase on areas where kangaroo rats were most abundant (Reynolds 1950). During a favorable seed year, and if range condition is at a level where the supply of large-seeded perennial grass seed is in excess of needs of kangaroo rats, much more seed is cached than is ever recovered (Reynolds 1958). Large seeded species have difficulty in germinating and establishing from seed on the soil surface and may require burial in seed caches for seedling establishment to occur (LaTourrette et al. 1971, Evans et al. 1983). Because seed left in the ground is in a more favorable environment for germination and early seedling survival than seed lying on top of the ground, the rate of plant restocking may be enhanced by the presence of kangaroo rats (Reynolds 1950, LaTourrette et al. 1971). Rodent caches of antelope bitterbrush, snowbrush (*Ceanothus velutinus*), squawcarpet (*C. prostratus*), green rabbitbrush (*Chrysothamnus viscidiflorus*), cheatgrass, and Indian rice grass (*Oryzopsis hymenoides*) have been reported (West 1968, LaTourrette et al. 1971, McAdoo et al. 1983). These

caches provide opportunities for germination of species such as bitterbrush and snowberry (*Symphoricarpos* spp.) on recently burned or denuded pinyon-juniper and sagebrush sites (Ferguson and Basile 1957, West 1968, Everett and Kulla 1976, Evans et al. 1983). Rodents also transport mycorrhizae associated with range plants and therefore could establish plant species and their associated mycorrhizae on denuded range sites (Maser et al. 1988).

McAdoo et al. (1983) observed that heteromyid rodents were very important in maintaining stands of Indian rice grass on rangelands. Kangaroo rats preferentially harvest and cache the largest, most germinable rice grass seeds, rejecting empty seeds and polymorphic forms with reduced germination potential. Germination was greatly enhanced by the rodent's removal of the lemma, palea, and pericarp that induced dormancy, and emergence of seedlings from these caches was the primary means of stand renewal of Indian rice grass.

As rangeland deteriorates to fair or poor condition, woody perennial shrubs increase and perennial grasses decline (Reynolds 1958, Brown et al. 1979b), increasing open areas that are believed (Rosenzweig 1973) to allow the kangaroo rat to see and avoid predators (Bartholomew and Caswell 1951). Merriam kangaroo rat populations then increase (Reynolds 1950). Kangaroo rats have been blamed for the increase of mesquite and cholla cactus (*Cylindropuntia* spp.) (Reynolds 1950) by dispersing seed through storage in caches and passage of the seeds through their digestive tracts (Parker and Martin 1952, Reynolds 1954). As grass declines on depleted rangelands, Merriam kangaroo rats increase, more mesquite is favored, followed by a continuing downward cycle of less grass and more rodents. Under these conditions, kangaroo rats can be an important factor in accelerating range deterioration and in very poor rangeland, kangaroo rat activity may be sufficient to prevent range recovery. When the supply of perennial grass seed is sufficiently low, kangaroo rats may consume the entire seed supply and mesquite can continue to increase even without cattle grazing (Reynolds and Glendening 1949). In this case, reducing kangaroo rat populations may be necessary to improve the rangeland. However, if rangelands occupied by mesquite are heavily grazed by cattle, mesquite will increase despite the presence of kangaroo rats, so it will not measurably improve the range to reduce kangaroo rat populations; it will be better to remove the mesquite source of seed. Once the mesquite is gone, perennial grass will increase and kangaroo rats will concomitantly decrease.

Reduction of kangaroo rat populations to increase forage is therefore justified biologically only where the density of perennial grass is low and can be increased by grazing management or range improvement practices. Reduction would also be warranted where artificial reseeding is being attempted with large-seeded plants and is being hampered by kangaroo rats (Reynolds 1950).

Kangaroo rats may prevent rangeland succession by maintaining a sub-climax type of vegetation. Brown and Heske (1990) found that long-term removal of a guild of 3 kangaroo rat species from a Chihuahuan Desert ecosystem led to the conversion of the habitat from shrubland to grassland. Twelve years after removal, density of tall perennial and annual grasses increased approximately 3 times and rodent species typical of arid grassland colonized, including harvest mice. Kangaroo rats

were a keystone guild: through seed predation and soil disturbance they had major effects on biological diversity and biogeochemical processes, favoring establishment of annuals and shrubs by selectively foraging on large seeds, and by seed caching and burrowing activities. At this site, the effects of excluding kangaroo rats were much greater than exclusion of cattle. This experimental site was near the natural transition zone from desert to grassland, so the magnitude of changes reported by Brown and Heske (1990) after kangaroo rat removal may not occur in other desert environments.

Management Considerations for Small Rodents

Because of previous overgrazing and concomitant loss of desirable grass, forb and shrub species, millions of hectares of degraded sagebrush-grass, chaparral, and pinyon-juniper rangelands are unable to reach their potential for livestock forage or wildlife habitat (Vallentine 1989). Seeding is commonly used for restoring depleted vegetation (Standley 1988). Efforts to rehabilitate these rangelands by direct seedings have often failed because rodents consume up to 98% of the planted seeds (Nord 1965, Nelson et al. 1970, Sullivan and Sullivan 1982). Reynolds (1958), Brown et al. (1979b), Inouye et al. (1980), and Price (1983) found that kangaroo rats prey selectively on large seeds and can be a significant cause of seeding failure when large seeds are planted. If seeds are smaller than 1.1 million/kg, kangaroo rats have no effect on seeding programs. Various methods have been tried for reducing the impact of rodents on seeded areas. The most common method is poisoning, but it often fails because of rapid rodent immigration (Sullivan and Sullivan 1984). Everett and Monsen (1990) recommended adoption of seeding strategies that mimic natural seed predation avoidance mechanisms, such as providing more seed along with sacrifice foods that can be used by the resident rodent population, planting in the spring when rodent populations are low, selecting seeds with low rodent preference, and using chemical repellents on seeds. Many studies show that certain rodents prefer particular species or sizes of seeds (Reynolds and Haskell 1949, Reynolds 1950, Lockard and Lockard 1971, Smigel and Rosenzweig 1974, Everett et al. 1978, Price 1983). Standley (1988) seeded plots with small and large grass seeds and found that large seed was removed but small seeds were still present 36 days after planting. He recommended that when site conditions and management needs allow a choice of plant species to seed, smaller seeds may provide better results. Kangaroo rats operate under an "optimal foraging" strategy where they preferentially harvest seeds from dense patches or clumps rather than dispersed seeds (Pyke et al. 1977, Price and Jenkins 1986). This suggests that seeds should be placed as randomly as possible (Richardson et al. 1986, Everett and Monsen 1990). Evans et al. (1983) reported that only 8% of randomly cached bitterbrush seed was found by rodents compared to complete removal of broadcast seed. Buried seeds are less preferred than seeds on the soil surface (Price and Jenkins 1986) so drilling seed may also discourage seed predation (Everett and Monsen 1990).

Rangeland site conversions can have large impacts on rodent populations. Common range site conversion treatments that

reduce cover and food availability for rodents include prescribed burning, spraying with herbicides, chaining, rotobating, and disking (Vallentine 1989). Following spraying with 2,4-D or rotobating of black sagebrush (*Artemisia nova*), populations of deer mice and Great Basin pocket mice remained near those of controls, but the least chipmunk disappeared from rotobated plots (Zou et al. 1989). Spraying sagebrush-grass ranges with 2,4-D had little effect on density of deer mice, but caused a sharp decline in northern pocket gophers and least chipmunks, and an increase in montane voles (Johnson and Hansen 1969). Density of deer mice and pocket mice dramatically increased the second year following chaining and windrowing of Utah juniper (*Juniper osteosperma*) sites (Baker and Frischknecht 1973). After burning in sagebrush communities (McGee 1982), rodent species that require large amounts of cover such as voles, western jumping mice, and masked shrew decreased in numbers; deer mice populations remained close to preburn conditions. Greater consideration needs to be given to effects of range site conversion on small rodents. A suitable approach to coordinate range and wildlife habitat management would be to determine characteristic small mammal species within grazing allotments, determine cover levels at which each species is reduced in abundance or distribution, and determine the percentage of overall habitats that should be maintained for these sensitive species.

LEPORIDAE: JACKRABBITS AND COTTONTAILS

The order Lagomorpha, with a fossil history dating back to the Oligocene (Hall and Kelson 1959), is composed of 2 modern families: Ochotonidae (i.e., pikas) and Leporidae (i.e., hares and rabbits). The hares and rabbits are found on grazed rangelands and will be considered in this chapter. Two genera of Leporidae occur in North America: *Lepus* (hares) and *Sylvilagus* (rabbits). Hares are larger and have precocial young that are born fully haired, while rabbits are smaller and have altricial young.

Jackrabbits are a prominent rangeland herbivore throughout the West. Two principal species occur on rangeland: the black-tailed jackrabbit (*Lepus californicus*) (Fig. 19) and the white-tailed jackrabbit (*Lepus townsendii*) (Fig. 20). The following descriptions are provided from the work of Jones et al. (1985). The black-tailed jackrabbit is slightly smaller, with a total length of 535-585 mm and weight of 1.8-3.2 kg, compared to the white-tailed jackrabbit, with a total length of 540-640 mm and weight up to 4.5 kg.

The general circadian activity pattern is described for black-tailed jackrabbits by Lechleitner (1958b) but is impacted by season (Smith 1990) and ambient temperature (Knowlton et al. 1968). During daylight hours jackrabbits rest in forms, shallow depressions in or under bushes (Vorhies and Taylor 1933). Their activity increases during the crepuscular and early nocturnal period as they forage. They become less active before dawn as they reingest their pellets (Lechleitner 1958b, Smith 1990).

Their home ranges (Burt 1943) have been variously reported. Lechleitner (1958b) found that in the Sacramento Valley of Cal-

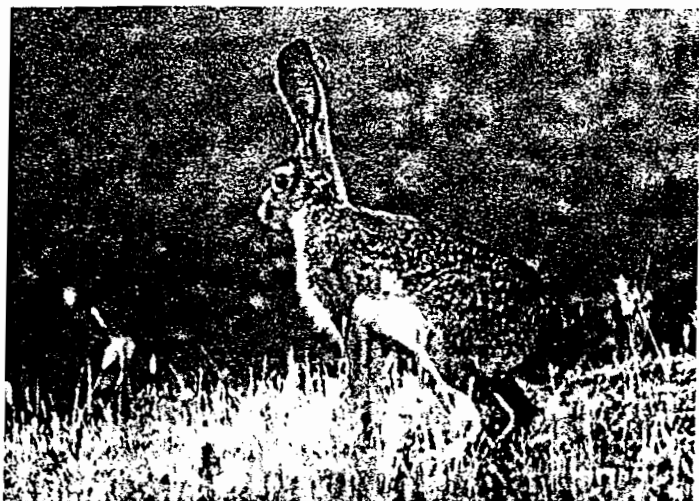


FIGURE 19. Black-tailed jackrabbit (*Lepus californicus*). Photo by G. Connolly.

ifornia, ranges were small and well defined, usually <20 ha, similar to those later reported by French et al. (1965) in Idaho (16.2 ha) and Tiemeier (1965) in Kansas (16.2 ha). Because home-range size is effected by the ability of the environment to provide food, shelter, and water, and their juxtaposition, it can be as large as several kilometers in diameter in grazing areas of Arizona (Vorhies and Taylor 1933). Orr (1940) reported jackrabbits feeding at distances up to 1.6 km from suitable cover. Donoho (1972) studied the dispersion of white-tailed and black-tailed jackrabbits on the Pawnee National Grasslands in northeastern Colorado and found that the white-tailed jackrabbits had significantly larger home ranges than black-tails. He reported males possessed larger home ranges than females; in contrast, Smith (1990) found no difference between the sexes in the home-range size of black-tailed jackrabbits. Also, seasonal and climatological influences effect the size and shape of jackrabbits' home ranges (Lechleitner 1958a, Tiemeier 1965, Gross et al. 1974, Smith 1990). These variables and others such as differences in procedures and analysis make home range generalizations and comparisons among studies difficult.

Jackrabbit densities as estimated by direct observation (Wywiałowski and Stoddard 1988), pellet census techniques (Taylor 1930, Arnold and Reynolds 1943), and radiotelemetry (Knowlton et al. 1968) are dependent on vegetation, climate, season, and other factors. Densities in Kansas have been reported from 35/ha in agricultural areas (Bronson and Tiemeier 1959), to 2.3/ha on mixed prairie (Brown 1947a), and 0.6/ha in western Kansas (Wooster 1935). Some of the lowest jackrabbit densities (0.01/ha) have been documented in southeastern Colorado (Flinders and Hansen 1973). This information conforms with findings of Fagerstone et al. (1980), who found jackrabbit densities significantly higher near cultivated crops than on isolated rangeland.

Fluctuations in jackrabbit density have been reported in the literature (Keith 1963, Gross et al. 1974) with cycles of approximately 5 to 10 years (Evans et al. 1970, Clark 1975). Populations in local areas can become extremely large during population irruptions (Fig. 21). Some researchers believe that



FIGURE 20. White-tailed jackrabbit (*Lepus townsendii*). Photo by K. Fagerstone.

the populations are not actually cyclic, but that drought and food availability (Bronson and Tiemeier 1959) or drought and overgrazing (Taylor et al. 1935) concentrate the hares. Evidence now suggests that the key parameters associated with population fluctuations are much more complex than previously thought. There appear to be geographic trends in jackrabbit frequency fluctuations (Clark 1972) and covariation with many interacting community components (Keith 1979, Johnson 1982, Hansson and Henttonen 1988) and natural phenomena like weather (Stoddard 1985). However, population fluctuations are not believed to be associated with a deviation in a 1:1 sex ratio (Lechleitner 1959, Gross et al. 1974, Griffing and Davis 1976).

Distribution

The black-tailed jackrabbit is the most common jackrabbit in the western and central United States (Fig. 22), ranging from the Pacific coast to western Missouri and Arkansas, and from the prairie and grassland regions of Idaho to South Dakota to the Mexican border (Hall and Kelson 1959, Hall 1981, Dunn et al.



FIGURE 21. Black-tailed jackrabbits (*Lepus californicus*) on Idaho rangeland during a population irruption. Photo from Denver Wildlife Research Archives.

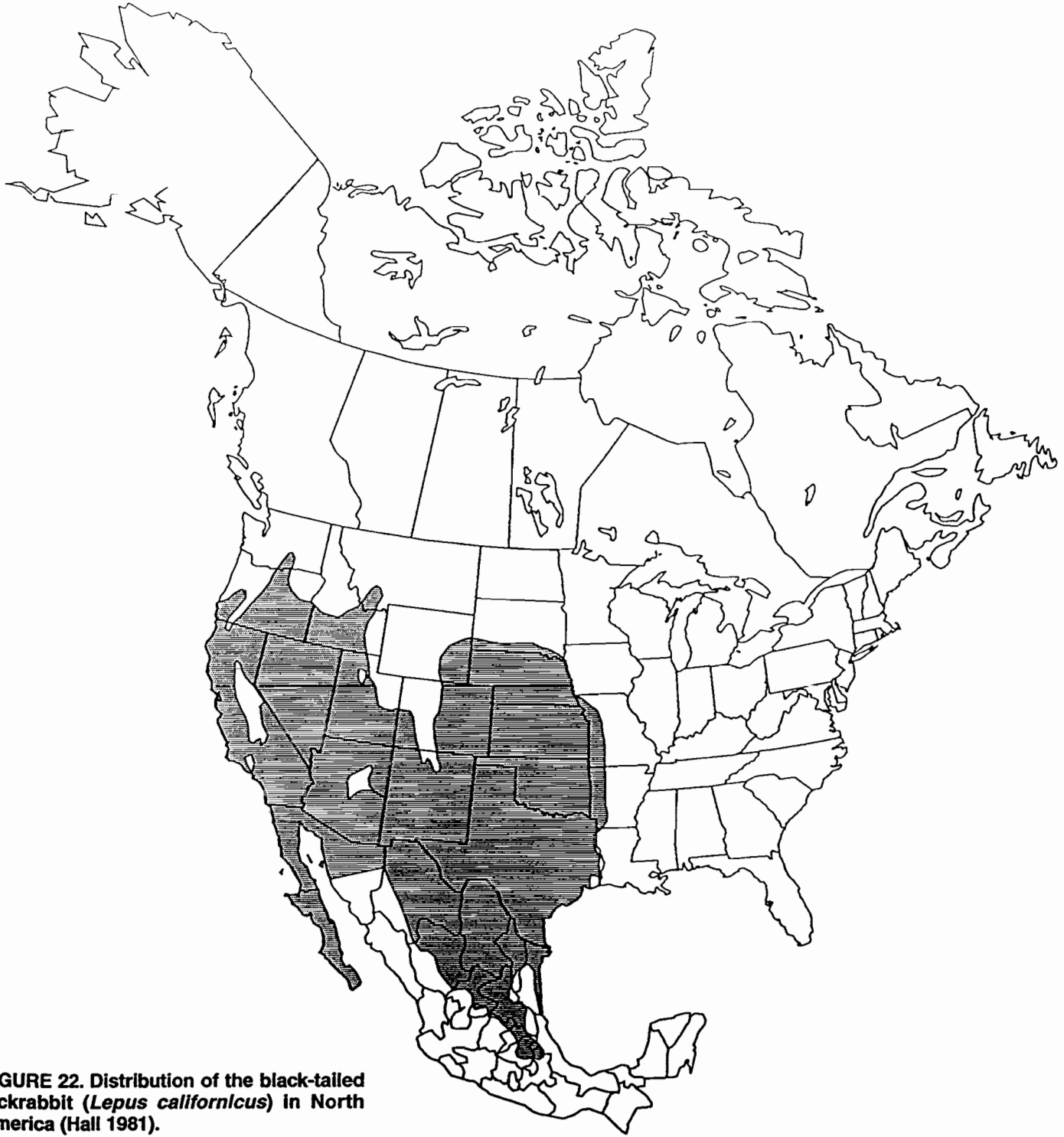


FIGURE 22. Distribution of the black-tailed jackrabbit (*Lepus californicus*) in North America (Hall 1981).

1982, Jones et al. 1985). Although the black-tailed jackrabbit occupies many diverse habitats, it is primarily found in association with shortgrass prairie and open country (Burt and Grossenheider 1959, Dunn et al. 1982). The black-tailed jackrabbit avoids areas of heavy brush or woods, where its principal means of defense, keen eyesight and speed of escape, are reduced (Jones et al. 1985).

The white-tailed jackrabbit occurs in close association with the flora of the northern Great Plains and open areas of the Great Basin (Hall and Kelson 1959, Hall 1981, Dunn et al. 1982,

Jones et al. 1985). They range from southern Canada to Colorado and from Michigan to the high mountain slopes of the Rockies, Cascades, and Sierras (Fig. 23). White-tailed jackrabbits once ranged south across the plains states to southern Kansas, but now occur generally north of the Platte River (Jones et al. 1985).

White-tailed jackrabbits prefer large expanses of croplands and pastures with interspersed brush and heavy vegetation in Iowa (Schwartz 1973), both upland and lowland grassland habitat in Colorado (Bear and Hansen 1966), and open flats and rye

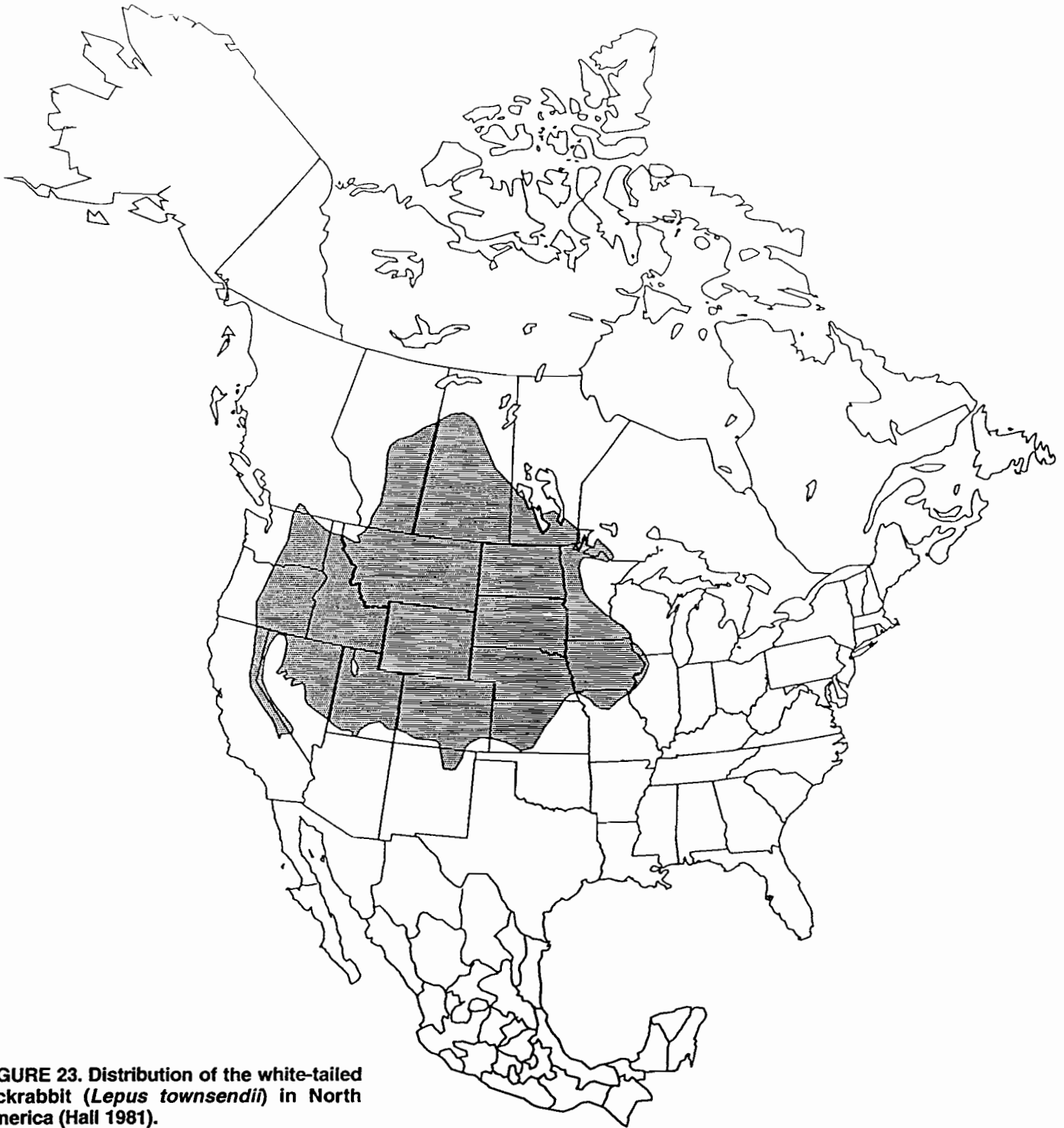


FIGURE 23. Distribution of the white-tailed jackrabbit (*Lepus townsendii*) in North America (Hall 1981).

grass in California (Orr 1940). In general, they avoid forests and woodlands. Leopold (1945) reported that in the early 1900s, the white-tailed jackrabbit was extending its range east into Wisconsin, Iowa, and Missouri, possibly as a result of the disappearance of the original forest cover (Kline 1963, and DeVoes 1964). In recent years, the white-tailed jackrabbit's range has declined, and it is now extirpated from Kansas (Hall 1955) and is rare in Missouri (Watkins and Novak 1973). Jones et al. (1985) suggested that these jackrabbits may be less well adapted to the general climatic warming of the Great Plains and less able to use

cultivated areas than the black-tailed jackrabbit. Carter (1939) and Brown (1947b) theorized that the expansion of black-tailed jackrabbits into areas formerly occupied by white-tailed jackrabbits was due to the changing habitat brought about by cultivation of the prairie by man. Flinders and Hansen (1972) and Donoho (1972) reported that when both species came into contact on the shortgrass prairie, the white-tailed jackrabbit selected more sparsely vegetated upland habitats and occupied higher elevations. In addition, Hansen and Flinders (1969) suggested that the black-tailed jackrabbit is more efficient than the white-tailed

jackrabbit in using feeding sites. Thus, the black-tailed jackrabbit, with its greater adaptability and feeding efficiency, may be able to displace the white-tailed jackrabbit.

Diet

Lechleitner (1958a) suggested that jackrabbits prefer to feed in open areas with a supply of succulent young plants, interspersed with patches of dense weeds; the open areas allow them to detect danger and the dense weeds serve as cover. Similarly, Orr (1940) found that jackrabbits prefer the margins of brush tracts adjacent to open areas. Foraging begins during the crepuscular period, increases during early night, and begins to decrease as dawn approaches (Lechleitner 1958b, Smith 1990). This general pattern of foraging is influenced by season (Smith 1990), ambient temperature (Knowlton et al. 1968), and phase of the moon (Lechleitner 1958a).

Black-tailed Jackrabbits. The diets of black-tailed jackrabbits have been studied by many scientists, especially in the Great Basin and Great Plains (Vorhies and Taylor 1933, Arnold 1942, Riegel 1942, Lechleitner 1958b, Currie and Goodwin 1966, Sparks 1968, Hansen and Flinders 1969, Flinders and Hansen 1972, Uresk 1978, Fagerstone et al. 1980, MacCracken and Hansen 1982, Wansi et al. 1992). These studies demonstrated that black-tailed jackrabbits are opportunistic feeders. However, Johnson and Anderson (1984) found that jackrabbits may feed more selectively than previously thought. Although the plant species eaten vary throughout the jackrabbit's range, their diets have some seasonal features in common: they show preferences for shrubs in winter and for grasses and forbs in the spring and summer (Hayden 1966, Westoby 1980). Various cereal crops (Lechleitner 1958a) and other cultivated crops (i.e., winter wheat [*Triticum aestivum*], alfalfa, crested wheatgrass [*Agropyron cristatum*],) (Flinders and Hansen 1972) are preferentially used when available. Fagerstone et al. (1980) documented that plant phenology was a major factor in determining food preferences of rangeland jackrabbits; 85% of their diets was composed of grasses in the spring, grasses and forbs were nearly equal in diets in early summer, and forbs and shrubs increased to 71% of the diets in late summer. In northeastern Colorado, black-tailed jackrabbit seasonal diets consisted mainly of grasses and forbs during summer and changed to shrubs during winter (Hansen and Flinders 1969). Grasses and sedges comprised 49% of their overall diet, with 7 plant species accounting for most of it (64%).

In contrast, Vorhies and Taylor (1933) found, in arid areas of the Southwest, that mesquite made up 54% of the annual diet. Uresk (1978) reported that needle-and-thread grass was preferred in sagebrush habitat, while yarrow (*Achillea lanulosa*) was preferred in bitterbrush habitat. Wansi et al. (1992) found that grasses comprised the largest component of jackrabbit diets in semidesert rangeland, particularly during the summer growing season. Lechleitner (1958a) observed that herbaceous weeds were not preferred dietary items. Most investigators agree that jackrabbits select for succulence (Hansen and Flinders 1969, McAdoo and Young 1980), particularly during times of water stress (Westoby 1980). Cooke (1982) and

Robertson et al. (1987) reported also that water may be a limiting factor in Australian rabbit populations.

White-tailed Jackrabbits. Bear and Hansen (1966) demonstrated seasonal dietary differences in white-tailed jackrabbits in southern Colorado. They ate 87% shrubs in the spring, including Parry's rabbitbrush (*Chrysothamnus parryi*) (70%) and fringed sage (*Artemisia frigida*) (15%). Summer diets consisted of forbs (70%), grasses (19%), and shrubs (7%). Fall diets were predominantly grasses (43%) and forbs (34%), with higher levels of shrubs (14%). Winter diets were primarily shrubs (76%). Flinders and Hansen (1972) found that white-tailed jackrabbits on the shortgrass prairie of Colorado fed mainly on plants in the prereproductive or early reproductive stages of development that had the greatest nutritive value and contained high proportions of moisture and crude protein. Flinders and Hansen (1972) also noticed seasonal differences in the diet of white-tailed jackrabbits. Early spring diets consisted of western wheatgrass and winter wheat, and western wheatgrass continued to be the most important food item during the summer (21%) and fall (46%). Winter diets were predominantly composed of winter wheat and crested wheatgrass.

Economic Status

Black-tailed jackrabbits have positive and negative relationships with humans. They are used for sport hunting, food, and fur (Jones et al. 1985). They are also an important part of the prairie ecosystem, and constitute a major food base for mammalian predators, particularly the coyote (Clark 1972). They have been reported to influence secondary succession in a positive way on old fields and denuded ranges by dispersing seeds in fecal pellets (Sparks 1968) and by increasing the viability of some seeds in their pellets by their digestive processes (Brown 1947a). Negative associations are related to situations where they are reported to cause extensive damage to agriculture (Hegdal 1966, Marsh 1984, Lewis and O'Brien 1990). Fagerstone et al. (1980) reported that cultivated crops adjacent to rangeland are particularly vulnerable to damage by jackrabbits, because the rangeland provides daytime resting areas for them. Jackrabbits have been reported to cause damage to seedling trees (Read 1971), grains and cotton (Vorhies and Taylor 1933), range rehabilitation programs (Wetherbee 1967), and vegetables (Bickler and Shoemaker 1975). Jackrabbit diseases that are transmissible to humans have also been reported, including tularemia (*Pasteurella tularensis*) (McMahon 1965) and (rarely) Rocky Mountain spotted fever (*Rickettsia rickettsi*) (Lechleitner 1959). On western rangelands they may be significant competitors with livestock.

White-tailed jackrabbits have had generally a more positive relationship with humans. Historically, some of the positive benefits of these jackrabbits were associated with sport hunting, food, and fur; their fur has been used commercially to make felt. They are also important to maintenance of ecological balance, biodiversity, and aesthetics on rangeland ecosystems. White-tailed jackrabbits do not cause much damage to agriculture (Jones et al. 1985), but do transmit diseases such as tularemia to humans.

Association with Livestock

The relationship between livestock grazing and jackrabbit population numbers is not well understood (Sanderson 1959, Short 1985) even though the combination can cause severe destruction to rangeland (Allen 1992). Some range scientists believe heavy grazing of rangeland increases suitable habitat for jackrabbits and encourages their presence (Brown 1947a, Jones et al. 1985). However, Taylor et al. (1935) reported that jackrabbits prefer moderately grazed pastures, and Norris (1950) stated that they prefer nongrazed rangeland. Short (1987) studied the interactive relationship of herbivores and their pastures and believes that herbivores affect the biomass, growth, and species composition of the pasture. As the density of herbivores increases, a point is reached when plant species of low quality and palatability also increase and make the pasture less suitable for all herbivores, including jackrabbits. Work by Hintz (1969) seems to support this view by concluding that rabbits are only 60% as efficient as ruminants in digesting fiber and therefore must feed on a high quality diet with < 40% fiber (Cooke 1974). Daniel (1991) studied the influence of range condition on the diets of jackrabbits and cattle. He found that: (1) jackrabbit densities were highest on good condition range, (2) range condition influenced the forb and shrub but not the grass diets of jackrabbits, and (3) jackrabbits consumed less grasses (ratio 1:3) and more shrubs than cattle, producing a moderate dietary overlap of 41%. Haskell and Reynolds (1947) reported that food consumption for black-tailed jackrabbits increased until they were 28 to 30 weeks of age then leveled off at an average consumption of 0.12 kg of air-dried native forage/day.

In early studies of competition, scientists estimated the foraging capacity of black-tailed jackrabbits to be: 1 cow equivalent to 148 black-tailed jackrabbits (Vorhies and Taylor 1933) or 62 jackrabbits (Arnold 1942), and 1 sheep equivalent to 6 black-tailed (Currie and Goodwin 1966) or 15 white-tailed jackrabbits (Bear and Hansen 1966). Sparks (1968) found that the greatest direct competition for forage between cattle and black-tailed jackrabbits was in early spring when both species preferred green forage such as western wheatgrass, needle-and-thread, and sunsedge (*Carex heliophila*), and least in late fall and winter.

Vegetation on many rangelands has changed during the last century, partly because of poor grazing practices (Martin 1975). Reports have documented shifts from grassland to shrub-dominated vegetation in New Mexico (Buffington and Herbel 1965), Nevada (Robertson and Kennedy 1954), and central Utah (Christensen and Johnson 1964) as a result of heavy grazing. Rice and Westoby (1978) observed that in Great Basin shrub communities protected for 15 years from domestic sheep, with or without protection from jackrabbits, plant community changes were slow to nonexistent, and that protection from jackrabbits had no effect.

Management

Jackrabbit management in the United States has generally focused on population reduction because of their crop depredation activities (Bronson and Tiemeier 1958, Hegdal 1966).

Beginning in the 1840s (Palmer 1896), organized rabbit drives were used to reduce populations; these have given way to issuance of hunting licenses as state game and fish departments began regulating jackrabbits as game species. Concurrently, the federal government employed or investigated a variety of control techniques such as biological control, habitat alteration, disease and parasites, mechanical control, and chemical control (Evans et al. 1970). Natural predators have not been effective in controlling jackrabbits (Palmer 1896, Horn 1941, Pressnall 1950, Lack 1954, Johnson 1964, French et al. 1965) and the introduction of new predators into an ecosystem has not been pursued because of high potential risks to other species (Howard 1967). Although the natural occurrence of enzootics in jackrabbits has been reported (McMahon 1965, Lechleitner 1959), they are not well understood. Disease and parasites have been used for jackrabbit control in other parts of the world. In Australia, the virus myxomatosis (*Myxomatosis*) was introduced in the 1950s for rabbit control (Ratcliffe 1951) with mixed results. Antifertility agents have been under investigation for years (Balser 1964, Howard 1967), but a variety of problems will need to be overcome before these agents can be used in the field, including: (1) current chemicals are not specific to hares, (2) most chemicals are only temporary in effectiveness, (3) carriers and baits are not yet available, and (4) public acceptance will be required (Evans et al. 1970). Several chemicals have been used in the past for jackrabbit control (McCabe 1966, Evans et al. 1970): thallium sulfate, sodium fluoroacetate, strychnine, zinc phosphide, and anticoagulants. All but zinc phosphide have secondary hazards (Evans and Ward 1967, Wetherbee 1967, Kaukenen 1982, Marsh et al. 1987, McIlroy and Gifford 1992, Ramey et al. 1992, Johnson and Fagerstone 1994). Of these, only zinc phosphide and the anticoagulants are currently registered for jackrabbit control (Johnston 1978, Ramey et al. 1992).

A variety of nonlethal controls like clean farming practices (Allen 1942), fencing (Evans et al. 1970), tree protectors (Johnson 1964), repellents (Johnson 1964, Welch 1967), predator odors (Sullivan and Crump 1986, Sullivan et al. 1988), and buffer crops or vegetative barriers (Lewis 1946) have been used to prevent damage from jackrabbits with some success. Evans et al. (1970) reported that alternate foods or lure crops failed to prevent damage to grain and hay crops during winter, and buffer crops 0.4 km wide or cleared land failed to protect crops when jackrabbit populations were high. However, Borrecco (1976) presented a successful example of habitat manipulation using an herbicide-induced reduction in vegetation cover and availability of summer foods that decreased the clipping damage to Douglas-fir seedlings (*Pseudotsuga menziesii*) by snowshoe hares (*L. americanus*). There is an obvious need for more information about jackrabbit population genetics, ecology, behavior, distributional changes, and livestock grazing interactions (Dunn et al. 1982).

COTTONTAILS

There are 2 primary species of cottontail rabbits: the eastern cottontail (*S. floridanus*) and the desert cottontail (*S. auduboni*) (Fig. 24). The eastern cottontail has a total length of 400-450

mm and a weight of 900-1,500 g. The desert cottontail has a total length of 390-435 mm and a weight of 950-1,375 g (Jones et al. 1985).

Distribution

Cottontails are among the most widely distributed of North American mammals. The eastern cottontail is the most widely distributed cottontail (Fig. 25). It is found from the eastern seaboard west to the Rocky Mountains and from southern Canada south to Costa Rica (Hall and Kelson 1959, Hall 1981, Chapman et al. 1982, Jones et al. 1985). It occurs throughout the plains region primarily in riparian ecosystems (Hall and Kelson 1959) and ubiquitously in the eastern deciduous forests. Lunk (1989) demonstrated a significant preference during their nocturnal foraging activities for farms rather than forested areas. Lord (1963) reported a circadian activity pattern similar to that of hares, but with nonsignificant nocturnal variation; however, Dalke and Sime (1941) have observed 2 pronounced feeding periods: the first, 3 to 4 hours after sunrise; and the second, from sunset to 1 hour later.

Home ranges for eastern cottontails are often sympatric and range from 2 to 6 ha (Chapman et al. 1980, Chapman et al. 1982). Reproductive fecundity is high, with litter sizes up to 12 (Kirkpatrick 1960). Densities as high as 17/ha (Chapman et al. 1982) to 25/ha have been reported (McKay 1978) with 8-10 year cyclic tendencies (Keith 1963, Bailey 1968). Cottontail densities are positively correlated with increased biomass of herbaceous vegetation and with areas ungrazed by livestock (MacCracken and Hansen 1982).

Desert cottontails are distributed widely throughout the arid areas of western North America (Fig. 26), from Montana south to central Mexico, and from the High Plains of Oklahoma, Kansas, and Nebraska to the Pacific Coast (Hall 1981, Jones et al. 1985). Typical habitat in the Great Plains includes weedy margins of fields and pastures, brushy areas, and dry ravines. Home ranges of desert cottontails average 0.4 ha (Trippensee 1934) to 1.2 ha (Allen 1938), with male home ranges much larger than those of females (Ingles 1941). The desert cottontail

has a high reproductive potential with an average litter size of 3.6 (Orr 1940), and it is capable of producing 2 to 3 litters annually and more than 1 generation annually (Ingles 1941).

Diet

The eastern cottontail has a diet that is cosmopolitan (Fitch 1947a), varying with the habitat and seasonal availability of forage (Chapman et al. 1982). Eastern cottontails prefer herbaceous plants when available during the growing season, including bluegrass, orchard grass (*Dactylis glomerata*) (Smith 1950, Dusi 1952, Klimstra and Corder 1957); timothy (*Phleum pratense*); clover (*Trifolium* spp.); and alfalfa (Dalke and Sime 1941). Succulent new growth supplies much of the cottontail's water requirements (Jones et al. 1985). Woody species like apple (*Malus pumila*) and red maple (*Acer rubrum*) (Dalke and Sime 1941, and Smith 1950) are preferred during the dormant season.

The desert cottontail is a crepuscular to nocturnal forager. Desert cottontails can survive droughts by obtaining water from cactus and forbs (Turkowski 1975). Orr (1940) found that they rely seasonally on grasses, sedges, rushes, shrubs (e.g., blackberry [*Rubis allegheniensis*]), and trees (e.g., willow [*Salix* spp.] and oak [*Quercus* spp.]). Hansen (1978) found that their annual diet was very similar to that of prairie dogs and cattle in the kinds of plants eaten, but differed in the relative proportions preferred.

Economic Status

Cottontails have provided a positive relationship with recreationists (Davis 1962) by providing small game hunting. Eastern cottontails are the most widely hunted game mammal in the United States (Jones et al. 1985) and their high reproductive rates allow them to withstand a high hunting pressure. Cottontails are a staple in the diet of various predators including coyotes, foxes, eagles, hawks, and owls (Fitch et al. 1946, Fitch 1947b, Capman et al. 1982). Badgers, weasels, and snakes take nestling young. Transmission of cottontail diseases to humans is of some concern (McMahon 1965). Eastern cottontails are responsible for 55% of tularemia cases reported in Americans (McDowell et al. 1964), due to direct contact while skinning and dressing animals. A few cases of plague (*Pasteurella pestis*) have also been reported in cottontail rabbits (Graves et al. 1978). Cottontails are not an important contributor to rangeland overgrazing. Overall, the ecological and economic and recreational benefits from hunting outweigh the minor damage done to crops, nurseries, and orchards (Chapman et al. 1982).

Rabbits have been suggested as seed dispersal vectors (Soriguer 1986) because of their high abundance, intensive use of small annual and perennial herbs, and production of fecal pellets. The literature has scattered reports of germinable seeds present in fecal pellets (Welch 1985, D'Antonio 1990), and Zedler and Black (1992) concluded that seed dispersal by rabbits may influence the distribution and long-term dynamics of some plant species.

Association With Livestock

Crouch (1982) reported that cottontails were significantly greater on the ungrazed bottomlands paralleling the South Platte



FIGURE 24. Desert cottontail (*Sylvilagus auduboni*). Photo by K. Fagerstone.



FIGURE 25. Distribution of the eastern cottontail (*Sylvilagus floridanus*) in North America (Hall 1981).

River in eastern Colorado and were almost nonexistent on grazed areas. Kundacli and Reynolds (1972) found that the desert cottontail is negatively impacted when pinyon-juniper habitat is cleared during operations for increased livestock production. Yet, preserving some combination of 175 to 225 downed, dead trees and living shrubs/ha maintained their numbers. Similarly, Green and Flinders (1980a) pointed out that the

removal of sagebrush for increased cattle production negatively affected the pygmy rabbit (*Brachylagus idahoensis*) because of their critical need for sagebrush (Green and Flinders 1980b).

Management

According to Chapman et al. (1982), the optimum habitat for the eastern cottontail in the Midwest is old, weedy, moderately

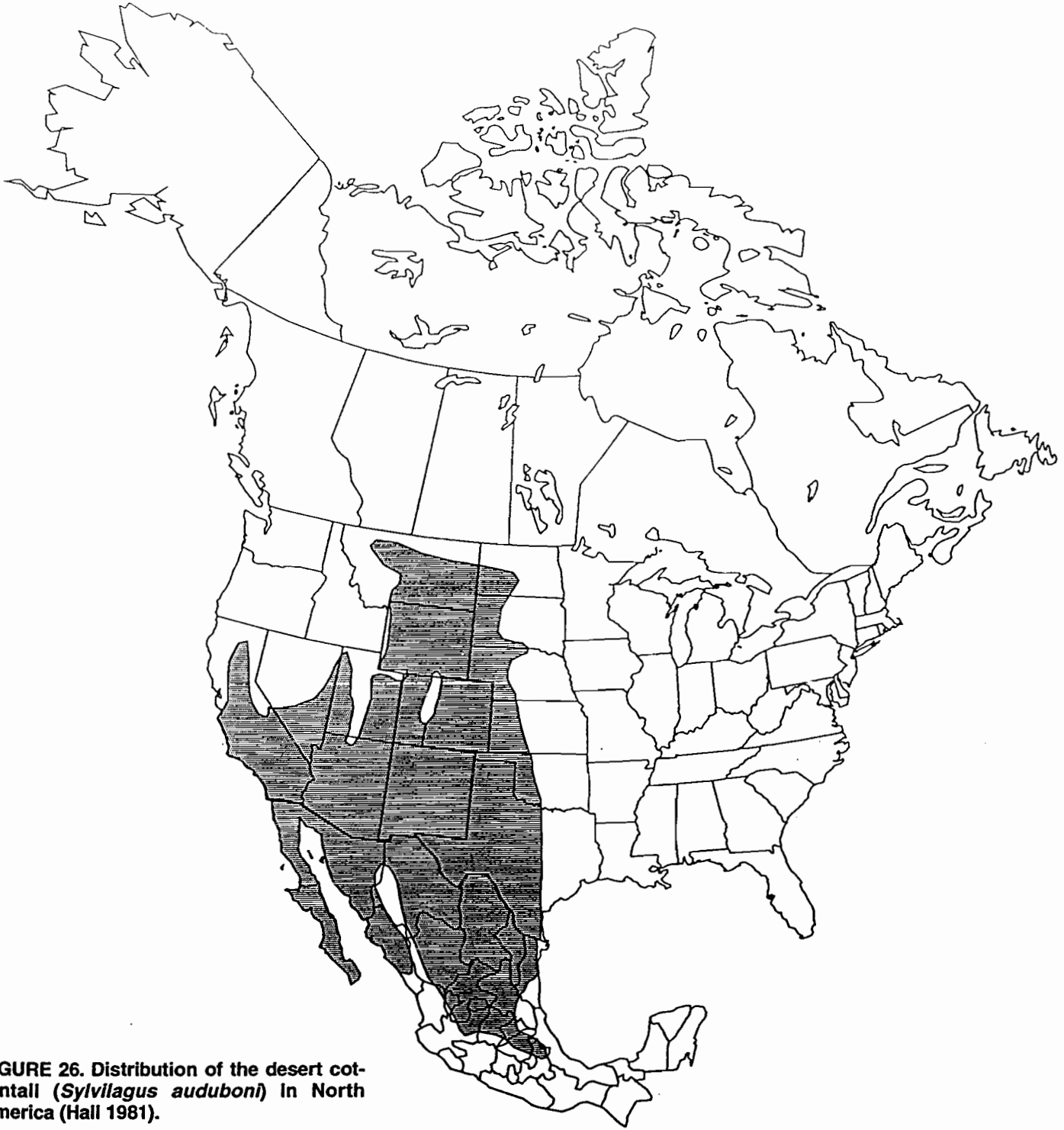


FIGURE 26. Distribution of the desert cottontail (*Sylvilagus auduboni*) in North America (Hall 1981).

grazed, unimproved, native grassland pasture with numerous dense clumps of thorny shrubs and small trees to provide escape cover. Vaughan (1972) documented the cottontail's need for protective cover, and Johnson and Hansen (1979) found them to be most numerous around rock piles. Habitat management to increase populations should emphasize this need for cover, and Madison (1959) suggested building brushpiles. Cottontails utilize primarily successional vegetation; therefore, habitat management techniques like prescribed burning and sharecropping

have been suggested by Ellis et al. (1969) to control succession and increase cottontail numbers.

When cottontails are found in high concentrations, they may damage crops, nurseries, and orchards. One of the principal means used by state game agencies for regulating populations of cottontails is annual hunting seasons (Craven 1983). Other selective controls include exclusionary methods such as tree trunk guards (Marsh et al. 1990), fencing, repellents, habitat modifications, and trapping (Craven 1983).

SUMMARY

Prairie dogs most frequently colonize sites that have been overgrazed or otherwise disturbed. Livestock grazing therefore promotes high prairie dog densities, and colonies tend to expand under heavy grazing. Depending on climatic factors, prairie dog colony expansion rates can be decreased by increasing vegetation cover around colonies through reducing grazing and human disturbance, and prairie dog colony expansion can be increased by increasing grazing or disturbance.

Prairie dogs can greatly alter rangeland. By digging extensive burrow systems they disturb soil and promote growth of disturbance-oriented vegetation. Because prairie dogs have a system of vigilance that depends on being able to see terrestrial predators at a distance, they clip shrubs and other tall vegetation that impedes visual detection. This in turn alters the habitat toward predominantly short grasses and annual forbs, rather than the taller grasses and shrubs characteristic of climax communities. Prairie dogs can cause negative and positive changes in rangeland. Negative changes include decreased forb and grass cover in colonies, higher silicon concentrations in grasses found in areas grazed by prairie dogs, and removal of plant biomass that could be used by cattle. Positive changes include increased plant species diversity, increased production of forbs and grasses caused by clipping, and better quality food and growing conditions inside prairie dog colonies. The economic effects of prairie dogs can be variable, according to the condition of the rangeland. Although considered pests, studies have shown that eradication of prairie dogs has little effect on increasing the amount of food available for cattle and is frequently not economically justified.

Prairie dog colonies provide important habitat for many other species of vertebrates, including the endangered black-footed ferret. Bison are attracted to prairie dog colonies as grazing sites because the vegetation associated with colonies may be more digestible and have a higher nitrogen content than the vegetation at uncolonized sites. Evidence continues to mount that prairie dogs are valuable components of the prairie ecosystem and that one of the management goals for prairie dog colonies should be the maintenance of biological diversity.

Ground squirrels are widely distributed on western rangelands. Their burrowing activities may have positive effects on rangeland by deepening soils, causing soil mixing, and improving the water holding capacity of soils. Many ground squirrel species on rangeland appear to benefit from livestock grazing and are most common on overgrazed ranges, where they can reach high densities. Several species have been considered pests on rangelands, including the California, Belding's, Richardson's, Wyoming, and Columbian ground squirrels, because their consumption and clipping activities can significantly reduce the amount of forage available to livestock. Management of ground squirrels on rangeland has traditionally emphasized use of toxicants; however, ground squirrels are an important part of rangeland ecosystems, and provide a significant part of the predator food base. Given the paucity of information on the effects of ground squirrels on rangeland and on livestock weight gain, further evaluations of rangeland, ground squirrel, and livestock interactions should be undertaken.

Pocket gophers usually prefer rangeland that is in good to excellent condition and may be reduced in numbers on areas heavily grazed by livestock. Like the prairie dogs and ground squirrels, pocket gophers may influence rangelands in positive and negative ways. They may reduce total standing crop biomass by 20% or more, and may alter plant species composition and abundance by differential consumption resulting from dietary preferences. Additionally, by creating soil mounds, feeding tunnels and underground food caches, pocket gophers influence the survival, growth, and biomass of surrounding vegetation. Their tunneling and mound-building activities cause an increase in bare ground, with gopher mounds commonly covering 5 to 15% of the ground surface. Mound building activities may bury vegetation and continually provide germination sites for early successional annual plant species. Mound formation may also be instrumental in maintaining a perennial dicotyledon plant component. Soil deposited by gophers may have a lower nutrient content than surrounding soil, but pocket gopher mound-building activity has a positive effect of increasing the biomass of the vegetation immediately surrounding each mound, partially offsetting lowered rangeland productivity.

The Leporidae (jackrabbits and cottontails) are important herbivores in North American agricultural and rangeland ecosystems. Black-tailed and white-tailed jackrabbits generally prefer open grasslands and agricultural areas and tend to avoid forests. Their relationship with humans have been viewed as positive and negative. Positive values are associated with their role in sport hunting, food and fur production, seed dispersal, ecological balance, biodiversity, and aesthetics. Negative values include their role in crop depredations, declining condition of rangeland, wildlife disease transmission, and competition with livestock for forage. Extensive investigations have been conducted regarding their diets; jackrabbits select succulent prereproductive vegetation when available, and show seasonal preferences for grasses and forbs during the growing season and for shrubs during the remainder of the year. Jackrabbits appear to have a positive effect on the biomass, growth, and species composition of rangeland flora at low densities, but reach a point at which their increasing densities produce lower quality and less palatable vegetation. Their competition with livestock is less than once thought, because recent studies have shown little seasonal and vegetation species overlap. Therefore, management practices now focus less on lethal population control and more on selective control (i.e., lethal and nonlethal) of depredating animals.

Cottontails have a more ubiquitous distribution in North America and a more cosmopolitan diet than jackrabbits. They provide recreation, a staple prey base for predators, seed dispersal, and ecological biodiversity. Overall, these benefits outweigh the minor damage they cause to crops, nurseries, and orchards. They are not considered competitors with livestock, because they prefer ungrazed to moderately grazed pastures with significant amounts of trees and dense shrubs providing escape cover. Management practices have emphasized either increased survival of cottontails through habitat management and the development of successional vegetation, or the selective use of controls such as exclusionary devices, habitat modifica-

tion schemes, or trapping. The niche for jackrabbits and cottontails on rangelands is presently being debated, with some viewing them as pests needing eradication, while others believe they are essential to global biodiversity in a natural world. Both views are often presented as inflexible alternatives and may be based upon a fundamental lack of knowledge. Additional research on the interactions between rabbits and hares, livestock and rangelands may serve to bring these diverging views closer together towards a common management strategy.

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